

# Bothalia

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# A taxonomic review of the dry-fruited species of *Anemone* (Ranunculaceae) in southern Africa

J.C. MANNING\* and P. GOLDBLATT\*\*

**Keywords:** *Anemone* L., classification, nomenclature, Ranunculaceae, southern Africa, taxonomy

## ABSTRACT

The three dry-fruited species of *Anemone* sect. *Pulsatilloides* subsect. *Alchemillifoliae* (Ranunculaceae) from southern Africa are reviewed, with full descriptions and nomenclature, including complete synonymy, taxonomic history with nomenclatural corrections, ecological notes, and distribution. *A. tenuifolia* (L.f.) DC. from the Cape Floristic Region is segregated as ser. *Pinnatifoliae* from the two summer rainfall species, *A. caffra* (Eckl. & Zeyh.) Harv. and *A. fanninii* Harv. ex Masters, which remain in ser. *Alchemillifoliae*, emphasising the strong vegetative differences between the two series.

## INTRODUCTION

Generic relationships of tribe Anemoneae DC. (Ranunculaceae–Ranunculoideae) have been the subject of intensive morphological and molecular investigations (Hoot *et al.* 1994; Ehrendorfer & Samuel 2001; Schuettelpelz *et al.* 2002; Hoot *et al.* 2012), resulting in the recent expansion of the circumscription of *Anemone* L. to include the small segregates *Barneoudia* C.Gay (3 spp.), *Hepatica* Miller (7 spp.), *Knowltonia* Salisb. (8 spp.), *Oreithales* Schldl. (1 sp.) and *Pulsatilla* Miller ( $\pm$  38 spp.) (Tamura 1993). Second largest genus of tribe Anemoneae after *Clematis* L., *Anemone* s. l. is diagnosed by the presence of one or more leafy, cauline involucres beneath the flower, and a perianth comprised of imbricate, petaloid sepals only. It includes  $\pm$  200 species distributed throughout the world, primarily in the Northern Hemisphere with only a modest representation on the southern continents, where  $\pm$  30 species are recorded mainly from montane regions with a temperate climate (Ziman *et al.* 2006). The austral representatives are concentrated in South America (12 spp.) and southern Africa (11 spp.), with *A. thomsonii* Oliver endemic to east tropical Africa and a handful of additional species in Indonesia and Australasia (Hoot *et al.* 2012).

*Anemone* in southern Africa traditionally included just three species with dry fruits, but has since been enlarged to 11 spp. by the recent transfer of the eight fleshy-fruited species of *Knowltonia* (Manning *et al.* 2009). Although previously treated in *Anemone* by some authors, this close-knit group of species was generally retained as a distinct genus on the basis of its compound inflorescences of relatively small flowers and its bacate or berry-like fruits. Phylogenetic analysis of plastid and nuclear DNA sequence data has now confirmed its

intimate relationship to the southern African *Anemone* species with dry fruits, with which it shares apomorphic pantoporate pollen, and all of the southern African species are now associated as subsect. *Alchemillifoliae* (Ulbrich) Hoot of *A.* sect. *Pulsatilloides* DC. (Hoot *et al.* 2012). The fleshy-fruited species, which constitute ser. *Knowltonia* (Salisb.) J.C.Manning & Goldblatt within subsect. *Alchemillifoliae*, have been well monographed by Rasmussen (1979) [as the genus *Knowltonia*]. This is not the case with the dry-fruited southern African species, which, as yet, have been treated only incompletely or superficially (De Candolle 1824; Pritzel 1841; Harvey 1860; Ulbrich 1906), most recently as part of a wide-ranging review of all austral species of *Anemone* (Ziman *et al.* 2006). Although very valuable, this latter treatment is nomenclaturally incomplete and also perpetuates some errors, notably the incorrect name and authors for *A. tenuifolia* (L.f.) DC., as well as containing some mistakes in typification. We provide a complete review of the taxonomy and nomenclature of the dry-fruited species of *Anemone* from southern Africa, including full synonymy, taxonomic history, ecological notes and distribution.

Taxonomic relationships among the dry-fruited southern African species of *Anemone* were first formalised by Ulbrich (1906), who segregated *A. tenuifolia* [as *A. capensis*] in the monotypic ser. *Pinnatifoliae*; retaining *A. caffra* and *A. fanninii*, the two rosulate species with unligified caudices and palmate leaves, in ser. *Alchemillifoliae*. This treatment, with an emphasis on morphology, was followed by subsequent authors until recently when Hoot *et al.* (2012) weighted phylogenetic considerations by including all three species in an expanded ser. *Alchemillifoliae* within subsect. *Alchemillifoliae*, arguing that the two leaf morphs of *A. tenuifolia* differed more from one another in DNA base sequences than did *A. caffra* from *A. fanninii*. There is no compelling morphological basis for this treatment, since *A. tenuifolia* is intermediate between ser. *Knowltonia* and ser. *Alchemillifoliae* in having the compound foliage of the former but the sericeous, fusiform achenes of the latter. The molecular topology retrieves ser. *Knowltonia* as sister to a clade in which *A. tenuifolia* is in turn sister to *A. caffra* + *A. fanninii* and is thus consistent with either classification. Significantly, however, the cladistic

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branches subtending *A. caffra* / *A. fanninii*, the two leaf morphs of *A. tenuifolia*, and the members of ser. *Knowltonia* in the molecular phylogram presented by Hoot *et al.* (2012) are all of similar length, indicating comparable levels of sequence divergence of the three lineages from their last common ancestor. This observation, coupled with the clear morphological and ecological differences among the lineages, prompts us to revert to the segregation of the dry-fruited species in two series, with the fleshy-fruited species comprising a third series. This classification, which incorporates both phenetic and phylogenetic information, seems more appropriate to us than the alternative that stresses the slightly closer phylogenetic relationship between the dry-fruited species over their obvious morphological diversity. We do not consider ser. *Knowltonia* further here, and readers are referred to the taxonomic revision by Rasmussen (1979) and the revised generic placement by Manning *et al.* (2009) for further details.

#### MATERIALS AND METHODS

All relevant types were examined, as well as all specimens from BOL, MO, NBG, PRE and SAM (acronyms after Holmgren *et al.* 1990), the herbaria housing the most comprehensive collections of southern African species. All species were also studied in the field.

#### TAXONOMY

**Anemone L.**, Species plantarum: 538 (1753). Type: *A. coronaria* L.

*Knowltonia* Salisb.: 372 (1796). Type: *Knowltonia rigida* Salisb., nom. illegit. = *Anemone knowltonia* Burt Davy

Perennial, rhizomatous herbs, rarely shrublets. *Leaves* basal, alternate, simple and palmate or ternately compound, toothed, petiole base sheathing; flowering stem with 1–5 whorls of 2–4, partly fused leaves. *Inflorescence* 1-flowered or of di- or tri-chasial, umbelliform cymes, the umbels and umbellules surrounded by involucre of compound or simple leaves. *Flowers* bisexual. *Sepals* numerous, petaloid, imbricate, deciduous, the outer usually differing slightly in colour, form and hairiness from the inner. *Petals* 0. *Stamens* numerous, centrifugal or centripetal. *Carpels* numerous, each with 1 pendulous ovule. *Fruitlets* clustered, usually achenes but sometimes drupes, glabrous to tomentose, rarely with a plumose, tail-like beak.

± 200 spp., cosmopolitan, mainly Northern Hemisphere; 11 spp. in southern Africa.

#### subg. *Anemone*

sect. **Pulsatilloides** DC., Regni vegetabilis systema naturale 1: 195 (1817). Lectotype, designated by Tamura (1995): *A. capensis* Lam., = *A. tenuifolia* (L.f.) DC.

subsect. **Alchemillifoliae** (Ulbrich) Hoot, Systematic Botany 37: 149 (2012). *A.* ser. *Alchemillifoliae* Ulbrich: 201 (1906). *A.* sect. *Alchemillifoliae* (Ulbrich) Tamura: 179 (1991). Lectotype, designated by Tamura (1995): *A.*

*caffra* (Eckl. & Zeyh.) Harv.

Plants with horizontal or ascending caudices. *Leaves* palmate or pinnately compound, toothed. *Inflorescence* simple or once- or twice-compound. *Flowers* with numerous (10–20) ± linear to narrowly elliptical sepals. *Achenes* numerous, usually four times longer than wide, glabrous or tomentose, dry or fleshy. *Pollen* pantoporate.

11 spp., temperate southern Africa

#### Key to series

- 1a. Leaves palmately lobed ..... ser. *Alchemillifoliae*
- 1b. Leaves ternately compound (rarely simple):
  - 2a. Inflorescence simple, 1-flowered (rarely with up to two secondary, involucrellate flowers); tepals larger, 20–40 mm long; fruits fusiform, dry, densely silky ..... ser. *Pinnatifoliae*
  - 2b. Inflorescence compound, several- to many-flowered; tepals smaller, 10–20 mm long; fruits ovoid or ellipsoid, ± fleshy, glabrous to puberulous ..... ser. *Knowltonia* [see Rasmussen (1979) for taxonomic account]

#### Key to dry-fruited species (ser. *Alchemillifoliae* and *Pinnatifoliae*)

- 1a. Subshrub with woody caudex; leaves ternately compound, sclerophyllous, glabrescent, margins revolute ..... 1. *A. tenuifolia*
- 1b. Rosulate perennials; leaves palmate, leathery, persistently pubescent, margins plane:
  - 2a. Plants smaller, peduncle 100–200 mm long; leaf blades (40–)60–100(–130) mm diam., mostly cleft less than halfway, usually thinly pubescent above and glabrescent or thinly pubescent beneath, mainly along nerves, rarely densely villous beneath, petioles 40–150 mm long; flowers 1(2), sepals dimorphic or ± monomorphic, outer usually only thinly sericeous beneath ..... 2. *A. caffra*
  - 2b. Plants larger, peduncle 200–800 mm long; leaf blades 150–350 mm diam., mostly cleft more than halfway, thickly velvety above and densely villous beneath, petioles 200–700 mm long; flowers (1)2–4, sepals dimorphic, outer ± densely sericeous or villous beneath ..... 3. *A. fanninii*

ser. **Pinnatifoliae** Ulbrich, Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 37: 239 (1906). Type: *A. capensis* (L.) DC., hom. illegit. = *A. tenuifolia* (L.f.) DC.

Evergreen subshrub with aerial, lignified caudex. *Leaves* pinnately compound or decompound, coriaceous, margins revolute. *Inflorescence* usually simple, 1-flowered, rarely compound with 1 or 2 secondary flowers each with individual involucre. *Achenes* fusiform, sericeous, walls dry.

1 sp., South Africa, Cape Floristic Region, mainly winter rainfall in fynbos.

1. **Anemone tenuifolia** (L.f.) DC., Regni vegetabilis systema naturale 1: 196 (1817); DC.: 18 (1824); Pritzelt: 613 (1841). *Atragea tenuifolia* L.f.: 270 (1782). *Clematis tenuifolia* (L.f.) Poir in Lam.: 298 (1812). *Pulsatilla tenuifolia* (L.f.) Spreng.: 664 (1825). *A. capensis* var. *tenuifolia* (L.f.) Harv.: 3 (1860); Ulbrich: 239 (1906). Type: 'Cape', Thunberg s.n. UPS-THUNB 12999 (UPS-THUNB—microfiche!, lecto., designated here).

*Atragea capensis* L.: 543 (1753). *Clematis capensis* (L.) Poir in Lam.: 296 (1812). *Anemone capensis* (L.) DC.: 195 (1817), hom. illegit. non. Lam. (1783); DC.:

18 (1824); Ulbrich: 239 (1906). *Anemone capensis* (L.) Harv.: 3 (1860), hom. illegit. non Lam. (1783); Ziman *et al.*: 207 (2006) [as *A. capensis* (L.) Lam.]. *Pulsatilla africana* Hermann ex Spreng.: 664 (1825), nom. illegit. superfl. pro *Atragene capensis* L. *Anemone arborea* [Hort.] Steud.: 95 (1840), nom. illegit. superfl. pro *Pulsatilla africana* [Hermann ex Spreng.]. Type: illustration “*Pulsatilla foliis trifidus, dentatis, flore incarnato, pleno*” in Burman: 148, t. 52 (1738), lecto!., designated by Oliver: t. 1569 (1969).

*Anemone capensis* Lam.: 164 (1783); Pritzel: 612 (1841). Type: ‘Cape’, without collector or date, *Herb. Jussieu* 10.536 (P-JU—digital image!, holo.)

*Atragene tenuis* Thunb.: 239 (1784). Type: not cited. Neotype: ‘Cape’, Thunberg *s.n.* UPS-THUNB 12999 (UPS-THUNB—microfiche!, neo., designated here).

[*Nomenclatural notes*: there is no indication that the specimen LINN 711.3, listed as the type of *Atragene capensis* L. by Killick (1977), constitutes original material. The typification of the name by Ziman *et al.* (2006) against an unspecified specimen in the Linnean Herbarium (LINN) presumably follows Killick (1977), but lacking the requisite specific intent cannot be treated as valid lectotypification in any event [Art. 7.11: McNeill *et al.* (2006)]. The typification by Ziman *et al.* (2006) of the supposed combination *Anemone capensis* (L.) Lam. against a ‘Thunberg & Ecklon’ specimen in Paris is inexplicable, not only by virtue of the fact that Ecklon arrived at the Cape half a century after Thunberg departed it, but also by the fact that a combination is automatically typified by the type of the basionym.

There is no specimen under the name *Atragene tenuis* in Thunberg’s herbarium nor is the species included in his *Flora capensis* (Thunberg 1823), but the name was treated as a synonym of *At. tenuifolia* L.f. by both Poiret (Lamarck 1812) and De Candolle (1818), and the concordance between the description of *At. tenuis* and that of *At. tenuifolia* in Thunberg’s *Flora capensis* is consistent with this interpretation. There is no reason to doubt that the two names apply to the same taxon and it is likely that both were in fact based on the same Thunberg collection. We therefore designate the specimen in the Thunberg herbarium as a neotype to fix this application. Although the specimen itself is not precisely localised, the collecting locality is cited as the Groot Winterhoek Mtns behind Tulbagh by Thunberg (1823) in his *Flora capensis*.]

Evergreen, rhizomatous subshrub with woody rootstock 10–15 mm diam., aerial stems erect, leafy, 15–150 mm long, simple or branched, partially covered with membranous or fibrous remains of old leaf bases. *Leaves* cauline, few to many, distant below but imbricate above, fully-developed at flowering, bi- to tritermately compound, ovate in outline, 40–120 × 30–100 mm, densely sericeous when young, glabrescent but persistently sericeous inside basal sheath, leaflets sessile or petiolulate, cuneate and 1–2 times pinnately lacerate or pinnate to bipinnate with needle-like segments 5–20 mm long, sclerotic, margins narrowly revolute, teeth or ultimate segments mucronate; petiole suberect, rigid, 15–100 mm long. *Inflorescence* 1-flowered, rarely compound with 1

or 2 secondary inflorescences, scape 60–500 mm long, 1.5–3.0 mm diam., thinly or densely villous; involucre bracts 3, entire or incised, 20–50 mm long, sometimes leaf-like with pinnatisect blade; pedicels 60–150(–220) mm long, villous. *Flowers* white to pale pink or mauve; sepals 12–25, dimorphic, narrowly elliptic or ± linear, 20–40 × 4–8 mm, obtuse to acute, outer wider and often longer than inner and densely sericeous beneath. *Stamens* centrifugal; filaments linear, 4–6 mm long, anthers 1.0–1.5 mm long, yellow. *Carpels* 4–6 mm long: ovary ovoid, 2–3 mm long, villous with hairs 1–2 mm long, style 2–3 mm long, subglabrous. *Infructescence* subglobose to shortly cylindrical, 15–20 mm diam. *Achenes* fusiform or arcuate, slightly compressed, 5–7 × 1.0–1.5 mm (excluding style), stipitate, densely sericeous with hairs 1–2 mm long (median hairs longest), style curved, ± 3 mm long, purple. *Flowering time*: mainly Aug. and Sept. but as late as Nov. at higher altitudes, rarely as early as Mar., mostly after fire. Figure 1.

*Distribution and ecology*: *Anemone tenuifolia* is largely restricted to the coastal slopes of the Cape Fold mountains, from the Bokkeveld Escarpment south to the Cape Peninsula and thence east to the Baviaankloof Mtns, extending inland along the southern coast onto the Kammanassie Mtns and the upper southern reaches of the Swartberg (Figure 2). It favours cooler, moister situations on south-facing slopes, typically in sheltered gulleys or in the lee of rocks, generally at moderate to high altitudes, 500–1 200 m but well above 1 500 m on the Swartberg and down to 300 m along the coast. Plants grow in moist, loamy soils, mostly on sandstone but also on granite, shale and limestone. Flowering has been recorded from autumn though summer but takes place mainly in winter and spring, and is strongly stimulated by a summer fire.

*Diagnosis and relationships*: the only dry-fruited winter-rainfall species of *Anemone* in South Africa, *A. tenuifolia* is a sclerophyllous, semi-shrub, with a distinctive, ± caulescent habit and glabrescent, bi- to tritermately leaves. The inflorescence is invariably 1-flowered and usually simple but occasionally compound, with one or two secondary, 1-flowered inflorescences developing within the primary involucre, each with a secondary involucre.

The species is highly variable in the degree of dissection of the leaves, which vary from biternate with cuneate, toothed or pinnatifid leaflets to tritermately pinnate leaflets divided into needle-like segments. The two extremes were, understandably enough, treated for some time as distinct species under the names *Atragene*/*Anemone tenuifolia* and *At./A. capensis* respectively, but with further collecting it is now clear that they represent part of the variation within a single species. The more highly dissected foliage morph is the most common and is found throughout the range of the species whereas forms with less-divided, biternate leaves are largely restricted to the extreme southwest, occurring on Table Mountain and adjacent mountain ranges, from Franschhoek to the Kogelberg. We have seen only one early collection of the less dissected leaf morph from outside of the southwestern Cape, from near Uitenhage (Ecklon & Zeyher 679).



A full range of leaf dissection can be found within a single population in the southwest, sometimes even within a single plant, with juvenile leaves tending to be less deeply dissected than those produced later (e.g. Manning 3361). This variation in leaf dissection among or even within individuals was first noted by Harvey (1860) on Table Mountain.

*History:* the first of the African anemones known to science, *Anemone tenuifolia* has a long history that has been vexed by nomenclatural confusion until today. Its first modern entry, in the *Species plantarum* under the name *Atragene capensis* (Linnaeus 1753), derives from a description and engraving [*Pulsatilla foliis trifidis, dentatis, flore incarnato, pleno*] published in Johannes



FIGURE 1.—*Anemone tenuifolia*, F. Anderson STE29969 (NBG, PRE). Artist: Fay Anderson. [Flowering Plants of Africa 60: pl. 1569 (1969)].

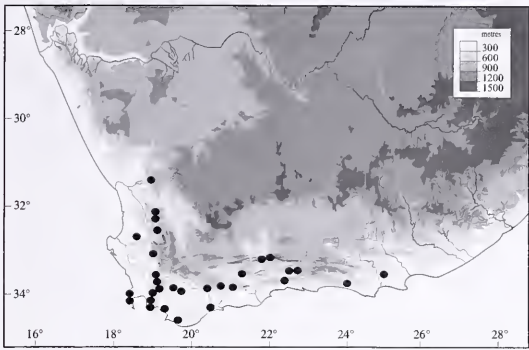


FIGURE 2.—Distribution of *Anemone tenuifolia*.

Burman's *Rariorum africanarum plantarum* (Burman 1738). The name was lectotypified against the Burman engraving by Oliver (1969), which depicts the form with biternate leaves. Burman's description includes references to both the *Codex Witsenii* and to Hermann's catalogue of African plants [*Pulsatilla Africana, Apii folio rigido, flore magno*]. The reference to the *Codex Witsenii*, which documents the natural history of Governor Simon Van der Stel's expedition to Concordia in 1685–1686 (Wilson *et al.* 2002), is perplexing as we find no reference to the species there. Paul Hermann (1646–1695), professor of Botany at Leiden, sailed for India in 1682 and called in at the Cape *en route*, where he made the first known herbarium collection of the local flora. *A. tenuifolia* is thus among the earliest elements of the Cape flora to become known to science.

Lamarck (1783) was the first to treat the species in the genus *Anemone*, under the name *A. capensis*, with an amplified description based on a specimen in De Jussieu's herbarium (now in P). Although it is possible that Lamarck merely intended transferring Linnaeus's name to *Anemone*, he refers in the protologue only to Hermann's polynomial and his name must therefore be treated as the new species *A. capensis* Lam., as was done by Pritzel (1841), with the De Jussieu specimen as the type (Oliver 1969). Ziman *et al.* (2006) are incorrect in treating Lamarck's name as the combination *A. capensis* (L.) Lam., based on *At. capensis* L.

This interpretation has several nomenclatural ramifications, most importantly that it precludes the transfer of *Atragene capensis* L. to *Anemone* by rendering any later combinations based on this name illegitimate later homonyms of *A. capensis* Lam. This was first done by De Candolle in his *Regni vegetabilis systema naturale* (De Candolle 1817) although most authors have mistakenly cited his later *Prodromus systematis naturalis regni vegetabilis* (De Candolle 1824) as the reference. In a further twist, Sprengel (1840) chose to follow Hermann in treating the species in the genus *Pulsatilla* as *P. africana* Hermann, a name that is rendered superfluous and illegitimate by Pritzel's citation of Linnaeus's *At. capensis* L. in synonymy. The correct name for the species in *Anemone*, based on *At. tenuifolia* L.f. as the next available name, is *A. tenuifolia* (L.f.) DC., as was established by Killick (1977), although again with the incorrect reference to De Candolle (1824).

In parallel with the proliferation of combinations for the form of the species with biternate leaves and cuneate segments matching the types of *Atragene capensis* L. and *Anemone capensis* Lam. was a similar multiplication of names for plants with more finely dissected, triternate leaves originally described as *At. tenuifolia* L.f. (1782). This name appears to be based on a collection made in the Groot Winterhoek Mtns by Carl Peter Thunberg (1743–1828), who later described the species separately under the name *At. tenuis* Thunb. (1784). It was only in the latter half of the nineteenth century that the two foliage morphs were treated as varieties of a single species by Harvey (1860), and taxonomic recognition at even this level was later abandoned by Killick (1977).

Additional specimens

NORTHERN CAPE.—**3119** (Calvinia): Lokenburg, (–CA), S slopes, arid fynbos, 28 Jul. 1956, *J.P.H. Acocks 18901* (NBG, PRE); S edge of Oorlogskloof Nature Reserve, 780 m, (–CA), 4 Sep. 2006, *N.A. Helme 4275* (NBG).

WESTERN CAPE.—**3218** (Clanwilliam); Piketberg, (–DC), *Ecklon & Zeyher 5 Pulsatilla africana* Herm. (SAM); Piketberg, Versveld Pass, (–DC), 19 Jul. 1941, *P. Bond 1028* (NBG), *E. Esterhuysen s.n. PRE 54537* (PRE). **3219** (Wuppertal): Krakadouw Peak, 4 700' [1 420 m], (–AA), Sep. 1936, *C. Thorne SAM52512* (SAM); Cedarberg, Welbedacht, 1 100 m, (–AC), Waboomveld boulder slopes SW aspect, 15 May 1986, *H.C. Taylor 11517* (NBG); Cedarberg, slopes below Tafelberg, 1 103 m, (–AC), 19 Sep. 2004, *F. Forest et al. 601* (NBG); Citrusdal, Die Trap, (–CA), 9 Sep. 1997, *M.W. van Rooyen, H.M. Steyn & A.J. de Villiers 720* (NBG). **3318** (Cape Town): Jonkershoek, (–DD), usually in rank grass/Protea veld in moister localities, Jul. 1965, *O. Kerfoot 5331* (NBG); Jonkershoek, Dwaarsberg, (–DD), damp places, 28 Aug. 1963, *J.J. Bos 473* (NBG); Klein Drakenstein, (–DD), Aug. 1934, *G.E. du Plessis s.n.* (NBG); Assegaaiboskloof, 1 300' [400 m], (–DD), TMS and granite, resprouting after burn, 16 Aug. 1962, *P. van der Merwe 1211* (NBG); Stellenbosch Mtn, kloof above Nietgegend, 403 m, (–DD), steep SW slope burned earlier in the year, 22 Sep. 1991, *E.G.H. Oliver 9896* (NBG, PRE). **3319** (Worcester): Tulbagh, Groot Winterhoek, (–AA), Apr. 1916, *E.P. Phillips 1098* (SAM); Ceres, (–AD), Aug. 1929, *C.L. Wicht 59* (NBG); mountains near Wellington, (–CA), Aug. [without year], *A.V. Duthie STE9050* (NBG); Du Toitskloof, (–CA), Sept. 1886, *Thode STE9263* (NBG); Slanghoek Mtns, Witteberg, 4 000' [1 200 m], (–CA), 21 Nov. 1943, *E. Wasserfall 642* (NBG); Du Toitskloof Pass, on Paarl side near top, (–CA), 24 Jul. 1953, *W.F. Barker 8029* (NBG); Du Toits Kloof, Molenaars Peak, (–CA), Oct. 1947, *T. Stokoe SAM63518* (SAM); Du Toitskloof Pass, Slanghoek Mtns, 597 m, (–CA), 22 Oct. 2008, *J.P. Roix 4447* (NBG); French Hoek [Franschhoek], 31 Oct. 1913, *E.P. Phillips 1063* (SAM); French Hoek Pass, (–CD), 7 Oct. 1946, *W.F. Barker 4126* (NBG); Devil's Peak, near waterfall, (–CD), Sep. [without year], *Ecklon & Zeyher Pulsatilla africana* Herm. (SAM); Cape Peninsula, Devil's Peak, Saddleback, (–CD), July 1886, *J. Thode s.n.* (NBG STE9265, PRE A69); Devil's Peak, (–CD), Aug. 1887, *J. Thode STE7780* (NBG); Devil's Peak, (–CD), 18 July 1956, *H.A. Baker 1107* (NBG); Table Mtn near Kirstenbosch, (–CD), Aug. 1882, *P. MacOwan 81* (SAM); Skeleton Gorge, (–CD), 18 Nov. 1897, *E.E. Galpin 3733* (PRE); 11 Sep. 1928, *J.B. Gillett 30* (NBG); Table Mtn, (–CD), 26 Oct. 1924, *H.M. Forbes 141* (NH); Table Mtn, top of Grotto Ravine, (–CD), 18 Sep. 1938, *R.H. Compton 7404* (NBG); Back Table, (–CD), Aug. 1972, *C.D. McKinnon 146* (NBG). **3320** (Montagu): Swellendam Mtn, 3 500' [1 060 m], (–CD), 4 Feb. 1941, *R.H. Compton 10601* (NBG); Swellendam, 10 o'clock Mtn, (–CD), May 1952, *T.M. Wurts 91* (NBG); Langeberg, alongside footpath to 10 o'clock Peak, S-facing slope, 800 m, (–CD), 1 Apr. 1987, *J. du Plessis 12* (NBG); Langeberg, Heidelberg, Lemoenshoek Peak, upper S slopes, (–DA), 19 Oct. 1966, *J.P. Rourke 628* (NBG); Lemoenshoek Peak, thick fynbos on wet steep slope, (–DA), 7 Dec. 1981 [sterile], *C.H. Stirton 10222* (NBG); Grootvadersbosch State Forest, near Helderfontein huts, 1 158 m, (–DD), cool SW-facing slope above stream, 17 Sep. 1985, *McDonald & Morley 956* (PRE). **3321** (Ladismith): Rooiberg, Ararat Ridge, 4 100' [1 242 m], (–CB), moist patch on SW slope, 18 Dec. 1977, *H.C. Taylor 9770* (NBG); Garcia State Forest, N slopes of Sleeping Beauty, 3 000' [900 m], seepage zone, (–CC), 9 Aug. 1977, *A.J. Lamb 16* (NBG). **3322** (Oudshoorn): Swartberg Pass, S side, steep rocky ridge, heathland, 1 415 m, (–AC), 9 Nov. 1977, *W.J. Bond 1130*



(NBG); Swartberg between Waboomsberg and Kanonberg, 6 000' [1 820 m], (–BD), dry grassy ledges and slopes just below summit, 30 Dec. 1969, *E.G.H. Oliver 3057* (NBG); George Div., Montagu Pass, Cradock Peak, (–CD), Jan. 1940, *H. Zimm s.n. SAM54812* (SAM); Kammanassieberg, 1 460 m, (–DB), along bank above road, recently burned, 4 Jul. 1990, *H.W. van Tonder68* (PRE); [Kammanassie Mtns], S slopes of Mannetjiesberg, 5 000' [1 510 m], (–DB), steep cool slopes at narrow altitude range, 19 Sep. 1954, *H.C. Taylor 1477* (PRE); upper TMS shaleband, 18 Sep. 1967, *J.P. Rourke 867* (NBG); 2 Oct. 1971, *E.G.H. Oliver 3606* (NBG). **3418** (Simonstown): Constantiaberg, (–AB), 18 Mar. 1943, *E. Wasserfall 147* (NBG); Orange Kloof, (–AB), 1 Aug. 1965, *F. Anderson STE29969* (NBG, PRE); Muizenburg, mountain, (–AB), Jul. 1922, *Anon STE15862* (NBG); Kalk Bay Mtn, 300 m, (–AB), upper slopes, 29 Sep. 1974, *P. Goldblatt 2833* (NBG); Somerset West, Helderberg Nature reserve, (–BA), recently burned, 15 Jan. 2012 [fruiting], *J. Manning 3361* (NBG); Somerset West, slopes of Haal Kop, (–BB), Aug. 1921, *J. Hauptfleisch STE1294* (NBG); Somerset Sneeuwkop, shale band facing SE, steep slopes, locally frequent in firebreak, 4 400' [1 330 m], (–BB), 16 Nov. 1969, *E.G.H. Oliver 3014* (NBG); Kogelberg, (–BD), Sep. 1953, *T. Stokoe SAM65791* (SAM); Kogelberg, SE slopes of Platberg, below rock overhang, moist, (–BD), 17 Aug. 1968, *C. Boucher 146* (NBG, PRE); Platberg, steep S-facing slopes in kloof, recently burnt, damp sandy/peaty soil, 2 000' [606 m], (–BD), 3 Dec. 1969 [fruiting], *E.G.H. Oliver 3035* (NBG); Betty's Bay, S-facing slopes near Leopard's Gorge, (–BD), 27 Oct. 1970, *W. Ebersohn 126* (NBG); Leopard's Kloof, in shade on S side of steep slopes, (–BD), 25 Nov. 1970 [flowering and fruiting], *W.F. Barker 10809* (NBG). **3419** (Caledon): Lebanon State Forest, Jakkals River, steep, moist S slope, 3 400' [1 030 m], (–AA), 1 Oct. 1980, *G. Forsyth 92* (NBG); Vogelgat, steep S-facing gully W of Castle Rock, 420 m, (–AD), 13 Sep. 1986, *I. Williams 3677* (NBG); Greyton, Perdekop, S slope in loamy soil, (–BA), 11 June 1982, *M. Viviers 415* (NBG); Riviersonderend, (–BA), Nov. [without year], *Ecklon & Zeyher Pulsatilla tenuifolia Spr.* (SAM); Riviersonderend Mtns, (–BB), Jan. 1949, *T. Stokoe SAM63519* (SAM); Riviersonderend Mtns, damp N slopes of Middelberg near top, (–BB), 11 Nov. 1997, *J. Manning 2144* (NBG); Riviersonderend Mtns, ridge W of Jonaskop, base of rocks in partial shade, 5 100' [1 545 m], 23 Nov. 1989, *E.G.H. Oliver 9336* (NBG); Groothagelkraal, limestone hills, local on S slope, (–DA), 24 July 1995, *P. Goldblatt & J.C. Manning 10209* (MO, NBG). **3420** (Bredasdorp): Potberg Mtn, steep S-facing slopes above deep kloof E of highest peak, damp peaty places, 500 m, (–BC), 28 Aug. 1979, *C. Burgers 2156* (NBG).

EASTERN CAPE.—**3324** (Steytlerville): [Tsitsikamma], Witte Els Bosch, mountain slopes above forest, (–CC), Sep. 1920, *H.G. Fourcade 926* (NBG); Baviaanskloof Mtns above Coutee's kraal, NW of Cambria, SE slope above kloof, 3 500' [1 060 m], (–DA), recovering from burn, 12 Sep. 1973, *E.G.H. Oliver 4536* (NBG). **3325** (Port Elizabeth): Uitenhage District, woods near Zwartkop River, (–CB), April [without year], *Ecklon & Zeyher 679* (SAM).

ser. *Alchemillifoliae* Ulbrich, *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 37: 201 (1906). Lectotype, designated by Tamura (1995): *A. caffra* (Eckl. & Zeyh.) Harv.

Deciduous, rosulate perennials. *Leaves* palmate, leathery, pubescent. *Inflorescence* simple, 1–4-flowered. *Achenes* fusiform, sericeous, walls dry.

2 spp., South Africa and Lesotho, summer rainfall montane grasslands.

2. *Anemone caffra* (Eckl. & Zeyh.) Harv. in *Thesaurus capensis* 1: 5 (1859); Harv.: 4 (1860); Ziman *et al.*: 208 (2006). *Pulsatilla caffra* Eckl. & Zeyh.: 59 (1834–1835). *A. alchemillifolia* E.Mey. ex Pritz. [as '*alchemillaefolia*']: 614 (1841), nom. illegit. superfl. pro *Pulsatilla caffra* Eckl. & Zeyh.; Ulbrich: 240 (1906) [as *A. alchimillifolia*]. *A. alchemillifolia* var. *caffra* (Eckl. & Zeyh.) Huth: 423 (1896). Type: [Eastern Cape], 'In colibus apricis, graminosis (altit. IV) apud sedes "Tyali" Caffrorum principis ad pedem "Chumni- et Winterberg" prope "Philippstown"', *Ecklon & Zeyher s.n.* (S—digital

image [S07-15770]!, lecto., designated here; TCD—JSTOR image! [TCD0001713—left hand specimen], K—JSTOR image! [K000075969, K000075971], P—JSTOR image [P00078546, P00078547]!, PRE!, isolecto.). [The S duplicate is selected as lectotype as being from Ecklon's personal herbarium, acquired by Sonder and now partly in S and partly in MEL (Glen & Germishuizen 2010).]

*A. alchemillifolia* var. *grandiflora* Huth: 423 (1896), syn. nov.; Ulbrich: 240 (1906). Type: [Eastern Cape], 'Bazaja [Bazija], near forests and elsewhere, 600–1 000 m al', without date, *R. Baur s.n.* (SAM, lecto., designated here). [The location of Huth's types is unknown (Stafleau & Cowan 1979) and the SAM specimen is selected as lectotype as being the only one known to us. It comprises two well-pressed plants. The locality information 'In graminosus summi montis Bazija, alt. 3 500–4 000' [1 000–1 200 m], Nov.' is essentially identical with that given in the protologue and there is no reason to doubt that it represents the same collection. An unlocalised Baur collection in BOL is probably a duplicate.]

*A. alchemillifolia* var. *schlechteriana* Huth: 423 (1896), syn. nov.; Ulbrich: 240 (1906). Type: [Eastern Cape], 'In graminosis mont Insiswa [Ntsizwa] ad 2 000 m alt.', 28 Jan. 1895, *R. Schlechter* (BOL, lecto., designated here.). [The location of Huth's types is unknown (Stafleau & Cowan 1979) and we select as lectotype the only duplicate known to us.]

*A. caffra* var. *pondoensis* Ulbrich: 240 (1906), syn. nov. Types: [Eastern Cape], 'Bisher nur Pondoland', *Bachmann 1527*, †B, syn.; *C. Beyrich 286*, †B, syn.). [The absence of these two specimens at B was confirmed by R. Vogt and they are presumably destroyed.]

[*Nomenclatural note*: The identification by Ziman *et al.* (2006) of the type of *A. caffra* (Eckl. & Zeyh.) Harv. as 'Katberg, 4 000–5 000', 9 Nov. 1832, *Drège 3571* (K, P) is incorrect. Ecklon & Zeyher (1834–1835) list only their collection cited above, which is thus clearly the type of the basionym. A Drège collection is, however, cited by Pritzel (1841) as a syntype along with the Ecklon & Zeyher collection in the protologue to his *A. alchemillifolia* (1841). The citation by Ziman *et al.* (2006) of a Berlin duplicate of the Ecklon & Zeyher collection as the type of *A. alchemillifolia* E.Mey. ex Pritz. without comment does not constitute valid lectotypification of the name [Art. 7.11: McNeill *et al.* (2006)], which is in any event nomenclaturally superfluous in including both the type of *P. caffra* and the citation of that name in synonymy [Art. 52: McNeill *et al.* (2006)]. Neither the Drège nor the Ecklon & Zeyher collections are extant at B (R. Vogt pers. com.).]

Deciduous, rhizomatous perennial with woody rootstock 6–10 mm diam., covered with fibrous remains of leaf bases. *Leaves* rosulate, 2–5, emergent or fully-developed at flowering, palmately (5–)7(–9)-lobed (rarely-parted), mostly less than halfway, blade (40–)60–100(–180) mm diam., orbicular-cordate in outline, leathery, thinly pubescent above, paler and glabrescent or thinly pubescent beneath, mainly along nerves, rarely densely villous, margin hispidulous and bidentate (rarely

sub-crenate) with 3–8 primary teeth along each side of lobes, teeth with reddish mucro; petiole erect or spreading, rigid, 40–150 mm long, sericeous. *Inflorescence* simple, 1(2)-flowered, scape (100–)120–150(–210) mm long, 2–4 mm diam., thinly or densely villous; involucre bracts 3 or 4, entire or incised, 20–50 mm long, sometimes leaf-like with trifid blade; pedicels (60–)100–250 mm long, villous. *Flowers* white or pale pink, the outer tepals sometimes flushed pink or purple beneath, or bright pink, sometimes with white centre; sepals 12–20, dimorphic or  $\pm$  monomorphic, narrowly elliptic or  $\pm$  linear, 20–40(–55)  $\times$  3–10(–18) mm, acute or obtuse, outer sometimes broader than inner and thinly to moderately densely sericeous beneath, often only basally. *Stamens* centrifugal; filaments linear, 5–7 mm long, anthers 0.8–1.5 mm long, yellow. *Carpels* 5–6 mm long; ovary ovoid, 2–3 mm long, sericeous with hairs 1.0–1.5 mm long, style 3–5 mm long, subglabrous. *Achenes* not seen. *Flowering time*: mainly Oct. to Nov., rarely earlier, flowering best after a winter burn. Figure 3.

*Distribution and ecology*: *Anemone caffra* is distributed throughout the mountains of the Eastern Cape from Grahamstown to Kokstad and inland on the Winterberg into southern Lesotho, with scattered collections further north along the foothills of the KwaZulu-Natal Drakensberg as far as Nkandla (Figure 4). Plants favour cooler, grassy or scrubby slopes, sometimes along watercourses, from 300–2 000 m but mostly below 1 500 m. Flowering is stimulated by burning of the veld the preceding winter.

The flowers are mostly moderately sized, with tepals 20–40  $\times$  3–8 mm, but plants from Nsikeneni Mtn near Kokstad (Abbott 7051) are especially handsome, with unusually large, white to pale pink flowers, the tepals 50–55  $\times$  10–18 mm. The species is also variable in flower colour. Usually white or sometimes pale pink, or the outer tepals flushed pink beneath, individuals with bright cyclamen pink flowers, sometimes with a white centre, occur in some populations. These striking colour morphs are relatively rare but have been recorded in the Eastern Cape from the Amatola Mtns and between eNgcobo and Kokstad, and in KwaZulu-Natal from Nkandla.

*Diagnosis and relationships*: distinguished from *Anemone fanninii* by its smaller stature, with smaller, mostly sparsely hairy leaves, the blades (40–)60–100(–180) mm diam. and lobed less than halfway, thinly pubescent above and glabrescent or thinly pubescent (rarely densely villous) beneath, mainly along the nerves, and mostly solitary-flowered scapes up to 200 mm long. The sepals are  $\pm$  monomorphic, the outer typically only thinly sericeous beneath. *A. fanninii* is a much more robust species with larger, densely velvety leaves 150–350 mm diam., and mostly 2 or 3-flowered inflorescences on stout scapes 200–800 mm long. The sepals are always distinctly dimorphic with the outer series broader than the inner and  $\pm$  densely sericeous or villous beneath.

Specimens of *A. caffra* from the Eastern Cape Drakensberg and southern Lesotho (viz. *Nienaber 1014*, *Schmitz 8848*, *Strever 1234*, *Victor 1591*) have the younger leaves (especially the lower surface) more densely pubescent than usual and have been confused with *A. fanninii*, especially individuals with two flowers

per stem, but are readily distinguished from that species by their much smaller, shallowly lobed leaves with relatively fewer (<10), proportionally larger primary teeth along each side of the lobes, and their generally shorter stature. The mature leaves in these populations are also not nearly as densely villous beneath as *A. fanninii*. We have not noticed any differences between the two species in the filaments (purportedly strongly expanded basally in *A. caffra*) nor carpel vestiture (basal hairs not distinctly shorter in *A. fanninii*) reported by Ziman *et al.* (2006).

The two species are essentially parapatric, with *A. caffra* distributed mainly south and east of *A. fanninii*, often at lower altitudes, but both occur around Polela, Qachas Nek and Mt Ayliffe, although they have never been recorded growing together.

*History*: *Anemone caffra* is one of many botanical novelties introduced to science by Christian Frederick Ecklon (1795–1868) and Carl Ludwig Zeyher (1799–1858). Arriving independently but almost simultaneously in Cape Town, the two Germans turned to plant collecting as a profession, both separately and together. In October 1831 they undertook a joint expedition to the present Eastern Cape, reaching as far as Queenstown, on which they encountered *Anemone caffra*. On their return to Cape Town the following year, Ecklon left for Germany and the Hamburg Botanic Garden to set about sorting their vast collection of material and the preparation of a joint publication on it, the *Enumeratio plantarum Africae australis extratropicae*. It is here that *Anemone caffra* was formally described in the genus *Pulsatilla*. The species was collected more-or-less simultaneously by another German, Johann Franz Drège (1794–1881), a trained horticulturist and active plant collector who had arrived in Cape Town in 1826. Drège undertook an extensive expedition into the Eastern Cape at the end of 1831 in the company of his apothecary brother Carl, finally returning to Cape Town in January 1836 (Glen & Germishuizen 2010). The two brothers collected the species on the Katberg in November 1832, and it was subsequently collected by many of the botanically inclined travellers to the eastern districts of the erstwhile Cape Colony during the latter half of the nineteenth century.

Drège listed the species as *Anemone alchemillifolia* in his *Zwei pflanzengeographische Documente* (Drège 1843). This was evidently a manuscript name given it by the Prussian Botanist Ernst Meyer, who wrote an introduction to the work. The species was subsequently published under Meyer's preferred but nomenclaturally illegitimate name by Pritzl (1841), who referred to both initial collections made by Ecklon & Zeyher and by Drège.

Minor variants among later collections from new localities in the Eastern Cape were seized upon as taxonomically significant entities by the Frankfurt botanist Ernst Huth (1896), who recognised var. *schlechteriana* for plants with smaller tepals ( $\pm$  20 mm long) collected in January 1896 on Mt Ntsizwa near Kokstad by the botanist Rudolf Schlechter (1972–1925), and var. *grandiflora* for a collection with larger tepals ( $\pm$  35 mm long) and lacinate involucre bracts made near Baziya,



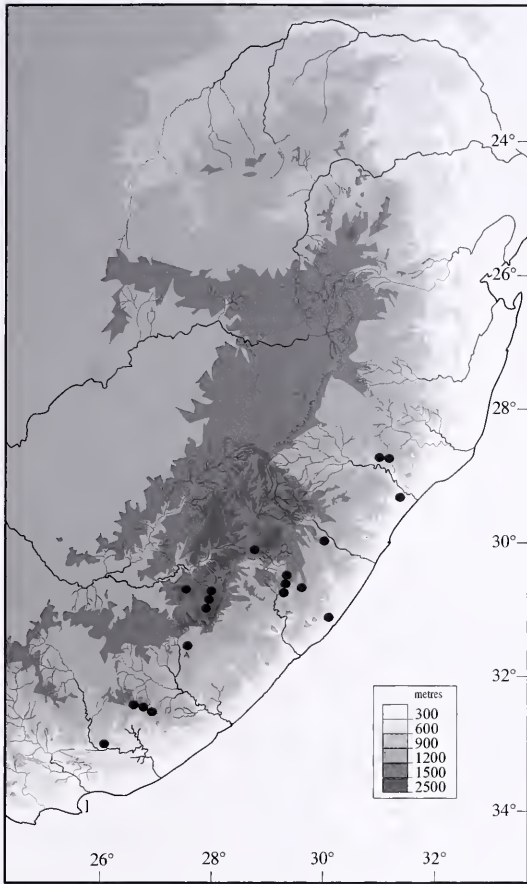
west of Umtata, by the missionary Leopold Richard Baur (1825–1889) sometime after 1873. It was during this year that Baur was visited at his mission station in Baziya by the Port Elizabeth businessman and amateur

botanist, Russell Hallack (1824–1903), who encouraged him to botanise the area and to send his collections to Peter MacOwan (1830–1909), principal of Shaw College in Grahamstown and expert on the regional flora.



FIGURE 3.—*Anemone caffra*. Artist: Auriol Batten. [*Flowers of southern Africa*. Fransden, Fourways. (1986)].



FIGURE 4.—Distribution of *Anemone caffra*.

Another form with less deeply lobed leaves was described as var. *pondoensis* by the Berlin botanist Eberhard Ulrich from two unlocalised and undated collections from Pondoland (Eastern Cape) made respectively by the medical practitioner and naturalist Franz Bachmann (1856 to ±1916) and one C. Beyrich, about whom nothing is known. Bachman spent only a year in Pondoland, over the period November 1887–November 1888, and would have collected the species during this time.

The first record of *Anemone caffra* outside of the Eastern Cape appears to have been made by John Medley Wood (1827–1915), Curator of the Durban Botanic Garden, who encountered it at Entumeni Mission south of Eshowe in KwaZulu-Natal in April 1888. It has now been collected from a few other localities in the province, but is still best known from the mountains of the Eastern Cape.

**Ethnobotany:** the species is used medicinally by Xhosa and Zulu as an emetic or an enema to treat biliousness (Watt & Breyer-Bandwijk 1932) and the powdered root is used as a snuff to relieve headache and toothache (Hutchings 1996). A decoction of the plant has purgative properties and is used in combination with *Athrixia heterophylla* (Asteraceae) to treat mental disease; the root is used as a love potion and to encourage breast development in young maidens (Batten 1986).

### Additional specimens

**LESOTHO.**—**3028** (Matatiele): after hilltop Ha Mokife, (–BB), steep grassy slopes near village, 28 Oct. 1979, *M. Schmitz 8848* (PRE); Qachasnek, 1 970 m, (–BB), dolerite outcrop W of road, flowers white, 4 Oct. 1988, *T. Streyer 1234* (NH).

**KWAZULU-NATAL.**—**2831** (Nkandla): Nkandla Forest, (–CA), 22 Sep. 1939, *J. Gerstner 3600* (NH); Nkandla village, (–CA), petals white, pink outside, 7 Dec. 1963, *J.W. Morris 397* (NU); Melmoth, Kataza, 3 000' [910 m], (–CB), S slope, 14 Jul. 1952, *H. Porter s.n.* (NBG); ± 10 km from Nkandla on Eshowe Road, (–CC), grassland, flowers white to deep pink, 27 Oct. 1996, *R. Williams & W. Menne 1367* (NH). **2929** (Underberg): Polela, (–DD), Nov. 1905, *Fernando 15* (NH); Mahwahqa Mtn, Sunset Farm, (–DD), 7 Nov. 1971, *M.A. Rennie 39* (NU); 10 Nov. 1973, *O.M. Hilliard & B.L. Burt 7169* (NU). **2931** (Stanger): Entumeni, (–AB), 12 Apr. 1888, *J. Medley Wood 3961* (NH). **3130** (Port Edward): Umtamvuna Nature Reserve, Smedmore, 420 m, (–CC), grassland E of forest, white, tinged pink, 29 Sep. 1983, *A. Abbott 1380* (NH); Umtamvuna Nature Reserve, 350 m, (–AA), vlei margin, flowers white, red below, 29 Aug. 1985, *A. Abbott 2713* (NH).

**EASTERN CAPE.**—**3027** (Lady Grey): near New England, Faskally Farm, N of farmhouse, 2 000 m, (–DA), foot of S slope of mountain, 9 Nov. 1995, *J.E. Victor 1591* (PRE). **3028** (Matatiele): Naudesnek, Philipsrust, edge of wetland in open grassland, 2 010 m, (–CA), 18 Oct. 1988, *T. Streyer 1465* (NH); Farm Mountain Side, ± 28 km NW of Maclear, 2 010 m, (–CC), in kloofie with stream, petals white to purple, 9 Nov. 1993, *S.P. Bester 1579* (NH). **3029** (Kokstad): Kokstad, Nsikeni Nature Reserve, Nsikeni Mtn, 1 900 m, (–AB), grassland, dolerite, white to pale pink flowers, 9–12 Nov. 1996, *A. Abbott 7051* (NH); Kokstad, Mt Currie Nature Reserve, (–AD), mountain side near stream, white flowers, 10 Nov. 1982, *T.A. Coleman 1038* (NH); Mt Currie, 1 700 m, (–AD), 11 Sep. 1990, *P.B. Taylor 149* (NU); Ongeluks Nek, (–CD), damp grassy slope, flowers white, 5 Dec. 1985, *O.M. Hilliard & B.L. Burt 18664* (NU); Mt Insizwa [Ntsizwa], (–CC), flowers white or pink, 17 Nov. 1973, *O.M. Hilliard & B.L. Burt 7294* (NU); Mt Ayliff, Ntsizwa Mtn, S slopes above pines, (–CD), flowers white to deep pink, 26 Oct. 1991, *E. Cloete 1196* (NH); Ngele, Umsilo Cutout, 1 200 m, (–DA), flowers white tinged purple below, 15 Sep. 1990, *A. Abbott 5345* (NH); Weza, Ngeli [Ngele], top of mountain towards Dakota Kop, 2 000 m, (–DA), moist grassland, white flowers tinged with pink, 3 Nov. 1997, *J. Arkell 416* (NH); 'in graminosis prope' [grassland near] Kokstad, (–DB), Oct. 1883, *Tyson 1568* (BOL, SAM); Dec. 1883, 'flores rosei' [rosy flowers], *W. Tyson 1845* (PRE, SAM). **3127** (Lady Frere): R56 ± 17 km out of Elliot to Ugie, Farm Trenmore, (–BD), 8 Nov. 2000, *E.P. Nienaber 1014* (PRE). **3128** (Umtata): ± 20 km NW of Ugie, Farm Fintana, 1 160 m, (–AA), 13 Sep. 1994, *S.P. Bester 2935* (PRE); Farm Tsitsa, ± 14 km S of Maclear, 1 220 m, (–AB), petals white, outer with some pink, 20 Nov. 1993, *S.P. Bester 1754* (NH). Tsolo, Ntywenka Pass, ± 4 500' [1 372 m], (–BA), highland sourveld, 17 Nov. 1945, *J.P.H. Acocks 12165* (PRE); Engcobo [eNgcobo], Satans Nek, grasslands W of summit, (–CA), flowers ranging from white to cerise, 23 Oct. 1991, *E. Cloete 1129* (NH); Cala, (–DA), slopes of kloof, Dec. 1942, *Whitworth s.n.* (BOL); Engcobo [eNgcobo], (–DA), flowers bright mauve-pink with white centre, 14 Oct. 1960, *L.F. Gibson s.n. NBG883/60* (NBG); hills near Engcobo [eNgcobo], (–DA), 8 Oct. 1961, *Esterhuysen 29159* (BOL). **3226** (Fort Beaufort): Katberg Pass, (–BC), Oct. 1963, *J.L. Sidey 3793* (PRE). **3227** (Stutterheim): Keiskammahock, Mtns N of Cata Forest Reserve, (–CA), level marshy areas, 4 Nov. 1948, *R. Story 3658* (PRE); Dohne Peak, (–CB), Jan. 1894, *T.R. Sim 1007* (NU); King William's Town, summit of Pirie, (–CD), Nov. 1893, 3 000' [910 m], *H.G. Flanagan 2207* (PRE, SAM); King William's Town, Dontsa Pass, 3 000' [910 m] (–CA), grassy bank, flowers white, 14 Nov. 1961, *A. Batten s.n.* (NBG); Pirie, (–CD), Nov. 1892, *Sim 110* (NBG, NU). **3326** (Grahamstown): Grahamstown, (–DB), Nov. 1897, *J. Glass 1802* (SAM); Grahamstown Hills, (–DB), Oct. [without year], *P. MacOwan 358* (SAM); Grahamstown, Featherstone Kloof, (–DB), 3 Oct. 1931, *J. Rennie & B. Rennie 169* (BOL).

**3. *Anemone fanninii* Harv. ex Masters** in Gardener's Chronicle 25: 432, fig. 84 (1886) [*A. fanninii* Harv.: 2 (1868), nom. nud.]; Hooker: t. 6958 (1887); Ulbrich: 240 (1906); Killick: t. 1441 (1965); Ziman *et al.*: 209 (2006) [as '*A. fanninii* Harv.']. Type: South Africa, [KwaZulu-Natal], 'Natal', *Adlam sub Masters 4/86* (K—JSTOR image! [2 sheets: K000075962,

K000075963], holo.). [The two sheets comprise respectively leaves and flowers and are evidently portions of a single collection.]

*A. fanninii* var. *parviflora* Ulbrich: 241 (1906), syn. nov. Type: [KwaZulu-Natal], 'in montibus Maritzburg' [Pietermaritzburg], without date, *Adlam s.n. sub Macowan & Bohus 1023* (SAM, holo.!; BOL! [2 sheets], iso.).

*A. fanninii* var. *mafubensis* Beauv.: 327 (1914), syn. nov. Type: [Eastern Cape], 'Griqualand East, Mafube', Nov. 1907, *H. Jacottet 93* (G—JSTOR image! [3 sheets: G00023697], holo.).

Deciduous, rhizomatous perennial with woody rootstock 10–18 mm diam., covered with fibrous remains of leaf bases. *Leaves* rosulate, 2–5, emergent or fully-developed at flowering, palmately (5–)7(–9)-lobed or -parted, mostly halfway or more, blade 150–250(–350) mm diam., orbicular-cordate in outline, leathery, velutinous above, paler and densely villous beneath with nerves very prominent, margin bidentate, with 15–20 primary teeth along each side of lobes, teeth with conspicuous reddish mucro; petiole erect, rigid, 200–700 mm long, villous. *Inflorescence* simple, 2- or 3(4)-flowered, flowers lacking involuclers, scape (200–)300–800 mm long, 4–6 mm diam., villous; involucler bracts 2–4(–6), entire or incised, 20–60 mm long, sometimes almost leaf-like with trifid blade; pedicels 70–300 mm long, villous. *Flowers* creamy white or flushed purplish on reverse, fragrant; sepals 12–20,  $\pm$  dimorphic, narrowly elliptic to elliptic, 25–60  $\times$  6–15 mm, obtuse or acute, outer series broader than inner and densely sericeous or villous beneath. *Stamens* centrifugal; filaments linear, 5–7 mm long, anthers 0.8–1.5 mm long, yellow. *Carpels* 7–9 mm long: ovary ovoid,  $\pm$  3 mm long, sericeous with hairs 1.0–1.5 mm long, style 4–6 mm long, subglabrous. *Achenes* not seen. *Flowering time*: mainly Oct. to Nov., rarely earlier, flowering best after a winter burn. Figure 5.

*Distribution and ecology*: *Anemone fanninii* is largely restricted to the eastern foothills and scarp of the central and northern Drakensberg in KwaZulu-Natal as far north as Witzieshoek in northeastern Free State; but is also recorded further south from Qachasnek in the southern Drakensberg and from Mt Ayliffe south of Kokstad in Eastern Cape (Figure 6). The species favours cooler, south-facing, grassy slopes, often along water courses or in seasonal seepages, from 600–3 000 m. Flowering is largely dependent on burning of the veld the preceding winter.

*Diagnosis and relationships*: closely allied to *Anemone caffra* but altogether more robust, with larger, thickly pubescent leaves, the blades 150–350 mm diam., velutinous above and densely villous or felted beneath, and mostly 2 or 3-flowered inflorescences on stout scapes (200–)300–800 mm long. The whitish sepals, sometimes flushed maroon on the reverse, are always  $\pm$  distinctly dimorphic with the outer series broader than the inner and densely sericeous or villous beneath. *A. caffra* is a smaller species with mostly thinly hairy leaves (rarely densely villous beneath, especially when young), 40–130 (–180) mm diam., and 1(2)-flowered scapes up to 200 mm long, typically with  $\pm$  monomor-

phic sepals, the outer mostly similar in size and shape to the inner and only thinly, or at most moderately, densely sericeous beneath. The flowers in both species vary significantly in size. We are not able to corroborate any differences between the two species in the filaments (purportedly strongly expanded basally in *A. caffra*) and in the carpel vestiture (basal hairs not markedly shorter than median in *A. fanninii*) reported by Ziman *et al.* (2006).

*Anemone fanninii* was deservedly described by Masters (1886) as a 'magnificent perennial' but despite his urgings it has not entered into general cultivation. Killick (1965) too recognised its promise as a garden subject but sadly observed that it had proven very difficult to cultivate away from its natural habitat. His hopes that horticulturists might soon discover its cultural requirements have so far remained unfulfilled.

*History*: the largest of the African anemones, *A. fanninii* commemorates local farmer George Fannin (1832–1865), who collected it in September 1863, shortly before his death, at his farm The Dargle in the KwaZulu-Natal midlands. Renditions of the name in the feminine form '*fanniniæ*' are thus incorrect. Fannin took a great interest in the plants around his farm, sending many interesting specimens to botanist and fellow Dubliner, William Harvey (1811–1866) at Trinity College, who reciprocated by naming several of the novelties after Fannin. Duplicates of Fannin's herbarium specimens are housed at Kew, the KwaZulu-Natal Herbarium, and at Trinity College. Unfortunately, Harvey's publication of the name *Anemone fanninii* in the second edition of his *Genera of South African Plants* (Harvey 1868) lacks a description and the name was only formalised by the publication of the description of a later collection (Masters 1886). This collection, from Polela in the Drakensberg foothills, stems from material gathered in December 1885 by the English horticulturist Richard Adlam (1853–1903), then resident in Pietermaritzburg. Seed that Adlam sent to England was flowered and the cultivated plant was described and illustrated in The Gardener's Chronicle Vol. 25 (Masters 1886). Maxwell Masters (1833–1907), editor of the magazine, provided the formal description and arranged for the fine engraving and is thus credited with the publication of the species. Masters sensibly lodged the flowers and leaves of the Adlam material in the Kew herbarium, and they comprise the type of the name, not Fannin's collection as indicated by Ziman *et al.* (2006), who erroneously attribute the species to Harvey.

Adlam, a fluent writer, contributed a popular article in the same issue of the *Gardeners' Chronicle* (Adlam 1886), vividly describing his rediscovery of the species. 'Next morning I started alone across country in search of a much talked-of plant', he writes, making it clear that his encounter was not a fortuitous one—news of this handsome anemone had clearly percolated among British horticulturists. 'The morning mists [after a heavy storm the previous night] still float and sweep along the higher ground, alternately hiding and disclosing the cattle feeding on a thousand hills. My path led along a hill side, where *Anemone fanninii* [*sic*] grew very strongly, flower stems 5 feet high, leaves 2 feet in diameter and flowers 2 inches across. Twenty years ago Harvey noted



it as a noble plant, yet I am not aware of its being in cultivation at home'. This was not quite true, for John Medley Wood (1827–1915), Curator of the Botanic Gardens in Durban, had sent living material of the species that he collected on the farm Ismont in 1883 to Kew. Received in June 1885, it was cultivated in a cool pit and flowered two years later, in April 1887, when it was beautifully illustrated in colour by the Kew artist Walter Hood Fitch (Hooker 1887).

Another, undated herbarium collection with smaller flowers collected by Adlam from the hills near Pietermaritzburg (possibly even from Fannin's original locality near The Dargle) and preserved in the South African Museum Herbarium (SAM), was described as var. *parviflora* by the Berlin botanist Eberhard Ulbrich (1906). A second variety, var. *mafubuensis* Beauv. (1914) is based on several beautifully pressed specimens collected at Mafube near Matatiele in the southern Drakensberg



FIGURE 5.—*Anemone fanninii*, Killick 3532 (PRE). Artist: Cythna Letty. [*Flowering Plants of Africa* 37: pl. 1441 (1965)].

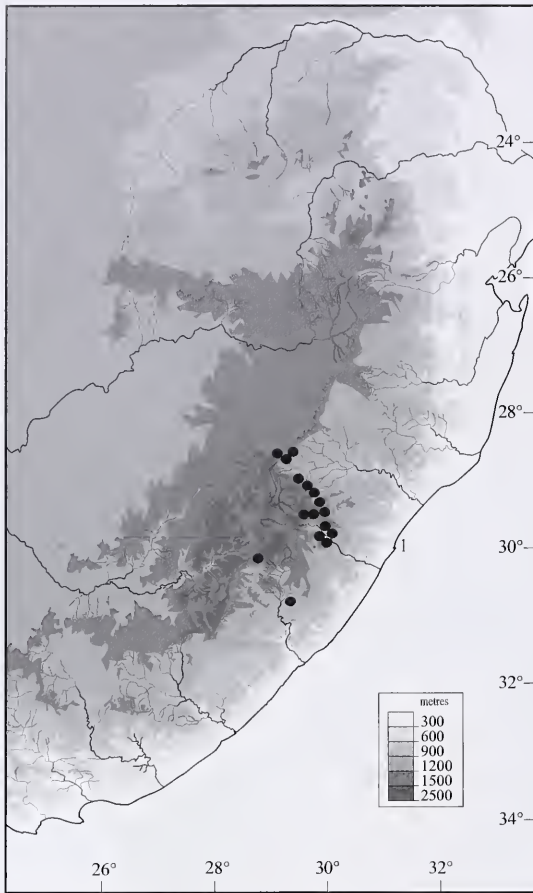


FIGURE 6.—Distribution of *Anemone fanninii*.

by H  l  ne Jacottet, sister of Dr Lautr   and the Rev. Edouard Jacottet. The unusually short flowering stems of these plants that attracted the attention of Gustave Beauverd (1867–1942), curator of the Boissier herbarium in Geneva, were artificially abbreviated by Mlle Jacottet in her pursuit of neatness and do not, as Beauverd thought, represent a naturally short genotype at all!

**Ethnobotany:** the roots are used in traditional Zulu medicine, probably in the same way as *A. caffra* (Hutchings 1996). The sap is recorded as acrid—like many members of the family the species presumably contains the bitter glycoside ranunculin, which is enzymatically converted when the fresh plant is bruised to protoanemonin, a toxic oil with an acrid taste that causes blistering of human skin.

#### Additional specimens

**FREE STATE.**—**2828** (Bethlehem): Elands River valley, near Mont aux Sources, (–DB), 1894, *Flanagan 2126* (BOL, NBG, NH, PRE, SAM); Mont aux Sources, 6 000' [1 820 m], (–DB), 27 Oct. 1897, *A. Bolus sub Guthrie 3974* (NBG); Goodoo Pass, (–DB), loose slope on veld, mixed with bracken fern, 15 Sep. 1915, *J.W. Bews 335* (NBG); Witziesshoek, scenic road, 8 500' [2 580 m], (–DB), grassy slopes, 9 Nov. 1969, *A. van der Zeyde s.n.* (NBG); Witziesshoek, 1 900 m, (–DB), damp, sheltered by rocks, 15 Sep. 1986, *A.G. Paton 305a* (PRE).

**KWAZULU-NATAL.**—**2828** (Bethlehem): [Natal National Park], Mahai River, (–DB), 26 Nov. 1924, *E.E. Galpin 10394* (PRE); near

Mahai Falls, (–DB), 2 Feb. 1955 [vegetative], *D. Edwards 580* (NU); Royal Natal National Park, (–DB), moist localities, Aug. 1964, *W.R. Transeld 276* (NU); Tugela Gorge, (–DB), 24 Aug. 1950, *B.E. Martin 448* (NBG). **2829** (Harrismith): Oliviershoek, (–CA), 11 Dec. 1980, *H.J.T. Venter 8486* (PRE); Cathedral Peak area, (–CC), steep slopes recently burned, Jul. 1946, *Esterhuysen 12923* (BOL). **2929** (Underberg): approaches to Champagne Castle, (–AB), Oct. 1947, *Whitworth s.n.* (BOL); Tabamhlope [Ntabanhlope], 6 000' [1 820 m], (–BC), 14 Oct. 1907, *J. Wylie com. J.M. Wood 10595* (NU, PRE); [Kamberg] Farm Culvers, 6 000' [1 820 m], (–BC), Dec. 1920, *F.A. Rogers 28266* (NBG, PRE); Giants Castle Game Reserve, (–BC), 20 Dec. 1987 [vegetative], *A.B. Cunningham 2719* (NU); Loteni Nature Reserve, (–BC), edge of watercourse, 9 Oct. 1978, *A.J. Phelan 139* (E, NU); 13 km from Himeville to Sani Pass, (–CB), Sep. 1973, *T.H. Arnold 530* (NH); Cobham Forest Station, Ndlovini, Frontbeck, 6 000' [1 820 m], (–CB), 8 Nov. 1980, *O.M. Hilliard & B.L. Burt 13363* (NU); Sani Pass, midway up pass along stream, (–CB), 1 Nov. 2006, *J.C. Manning 3076* (NBG); Impendhle, Deepdale, (–DB), Oct. 1918, *T.R. Sim s.n. PRE54549* (PRE); Impendhle, (–DB), 15 Nov. 1924, *C.E. Levett 89* (NH); 4 km before Impendhle after Nottingham Road, (–DB), burnt open grassveld, Sep. 1973, *T.H. Arnold 521* (PRE). **2930** (Pietermaritzburg): The Dargle, (–AC), Sep. 1863, *G.F. Fannin sub J. Sanderson 1170* (NH); Kunhardt's farm, 21 km from Merrivale on Boston Rd, (–AC), 1982, *C. Kunhardt 147* (NH); near Richmond, (–AC), 25 Oct. 1906, *J. Medley Wood 10 844* (NH); Byrne Valley, Minerva Private Nature reserve, 1 478 m, (–AC), 19 Oct. 2000, *R.N. Ntuli 204* (NH). **3028** (Matatiele): Qachas Nek, 6 000' [1 820 m], (–BA), mountain grassland, 30 Sep. 1962, *R.G. Strey 4316* (NH). **3030** (Port Shepstone): [Mid Ilovo], Ismont, (–AB), 2 000' [600 m], April 1883, *Medley Wood 317* (SAM). Uncertain locality: Yorkshire Wolds, edges of bush near streams, Sep.–Oct. 1918, *J. Thode s.n. STE4835* (NBG); Spitzkop, Emongweni bushy places near streams, juice acrid, Oct. 1890, *J. Thode s.n.* (NBG, NU).

**EASTERN CAPE.**—**3029** (Kokstad): Clydesdale, (–BA), Dec. 1884, *W. Tyson 2009* (BOL, SAM); Mt Aylliffe, (–CD), *M. Courtney-Latimer s.n.* [photo only] (NBG).

#### ACKNOWLEDGMENTS

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# Pollen morphology of members of southern African *Boerhavia* and *Commicarpus* (Nyctaginaceae)

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**Keywords:** acetolysis, *Boerhavia*, *Commicarpus*, Namibia, Nyctaginaceae, pollen morphology, SEM, South Africa, TEM

## ABSTRACT

In southern Africa, *Boerhavia* L. and *Commicarpus* Standl. are the most species-rich genera of the Nyctaginaceae. Hitherto, the pollen morphology of only three southern African species of each of these genera has been described. A palynological study of the remaining species is therefore necessary to complete the information for the taxa. The pollen morphology of sixteen species was studied with light, scanning electron and transmission electron microscopy. Pollen grains of *Boerhavia* and *Commicarpus* are uniform in shape and sculpturing. Grains are spheroidal and pantoporate, and the tectum tubuliferous and spinulose. Pollen grains of the *Boerhavia* are 52–91 µm in diameter and those of *Commicarpus* 52–129 µm. Spinules in both genera are 1–5 µm long. Pore plates have one or two spinules. In both genera the exine is 3.5–11.5 µm thick, the tectum 0.9–3.9 µm thick and the collumellae 0.6–2.8 µm long. Foot layers are 0.9–5.1 µm thick and the endexine is barely visible. Size variation of the pollen grain, pore diameter and exine thickness overlap and cannot be used to distinguish between the two genera or the individual species.

## INTRODUCTION

Nyctaginaceae Jussieu, commonly known as the four-o'clocks, are a relatively small family of about 30 genera and 300–400 species (Levin *et al.* 2001; Douglas & Manos 2007). It is distributed throughout the tropical and subtropical regions of the New World (Bittrich & Kühn 1993; Jordaan 2000), but mainly in the Americas (Stannard 1988). In southern Africa, south of the Zambezi River (Botswana, Lesotho, southern Mozambique, Namibia, South Africa, Swaziland and Zimbabwe), five genera and 20 species occur of which sixteen species are found in Namibia (Germishuizen & Meyer 2003; Struwig 2012). Namibia is therefore the centre of diversity for the family in southern Africa. *Boerhavia* L. and *Commicarpus* Standl. are the largest genera of the family in southern Africa, with seven and nine species respectively (Germishuizen & Meyer 2003).

Pollen grains of Nyctaginaceae are 17–200 µm in diameter, spheroidal, prolate or oblate and 3(4)-colpate, pantocolpate or pantoporate (Bittrich & Kühn 1993). Pores are covered by a pore plate, which can either be roughened or spinulose (Bittrich & Kühn 1993). The exine is very thick and varies in sculpturing (spinulose, tubuliferous or coarsely reticulate) (Nowicke 1970; Bogle 1974).

Heimerl (1934) used pollen morphology to divide the Nyctagineae into four subtribes. Subtribe Nyctagininae (to which *Boerhavia* and *Commicarpus* belong) is characterised by large, spheroidal, pantoporate pollen grains with thick walls and a tubuliferous and spinulose exine (Nowicke 1970; Nowicke & Luikart 1971). Nowicke (1970) found that the shape and size of the grains, and the thickness of the exine, form a continuum within gen-

era and species of subtribe Nyctagininae, so much so that these characters are of limited taxonomic significance. Nowicke & Luikart (1971) came to the same conclusion for the other subtribes. Recently, a phylogenetic study of the family (Douglas & Manos 2007) found that pollen morphology is homoplasious among genera and can therefore not be used to support the tribal and subtribal divisions of Heimerl (1934).

Pollen grains of 13 of the 40 species of *Boerhavia* and three of the 35 species of *Commicarpus* were described by Nowicke (1970) as spheroidal, pantoporate and the sexine as tubuliferous and spinulose. The spinules are 1.0–2.5 µm long. Grains of *Boerhavia* are 70–138 µm in diameter, with 18–40 pores. Pores are 2.4–7.0 µm in diameter and the pore plates have a roughened base with 1 or 2 spinules. Sexine is 2.5–6.0 µm thick and the nexine is 4–7 µm. Grains of *Commicarpus* are 84–112 µm in diameter with 27–39 pores. Pores are 3.0–5.5 µm in diameter and the pore plates have 1 or 2 spinules. Sexine is 2.5–5.5 µm thick and the nexine is 2.5–5.5 µm.

Pollen of southern African members of *Boerhavia* and *Commicarpus* has not been described extensively, except for the naturalised *B. diffusa* var. *diffusa* and *B. erecta*, and the native *B. repens* subsp. *repens*, *C. fruticosus*, *C. helenae* var. *helenae* and *C. pentandrus* (Nowicke 1970; Perveen & Qaiser 2001). A palynological study was therefore conducted to provide a detailed description of the pollen morphology of other native members. As previous studies (Nowicke 1970; Perveen & Qaiser 2001) have suggested that pollen morphology of these two genera is uniform and of limited taxonomic value at the generic or species level, the poorly known southern Africa species provided an opportunity to report further evidence regarding the taxonomic significance of palynological characters.

## MATERIALS AND METHODS

Pollen from herbarium specimens and fresh plant material collected *in situ* in Namibia and South Africa

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was investigated with light microscopy (LM), scanning electron microscopy (SEM) and transmission electron microscopy (TEM).

Pollen grains were acetolysed according to the method of Erdtman (1969). For LM, pollen was mounted in glycerine jelly and sealed with entellan (Product 7961, E. Merck, Darmstadt) according to the method of Fripp (1983). For SEM, a drop of 96% ethanol/pollen mixture was pipetted on specimen stubs, dried and sputter-coated with gold/palladium. Specimens were examined with a FEI Quanta 200 Environmental Scanning Electron Microscope (ESEM) or a JEOL JSM 840 SEM. A minimum of eight pollen grains from three individuals per species were used to measure the diameter of the grain, pores and the length of the spinules.

For TEM, unacetolized grains were fixed in 4% aqueous paraformaldehyde and rinsed in three changes of 0.05 M cacodylate buffer, pre-stained in 2% uranyl acetate (pH 2), dehydrated in a graded ethanol series and embedded in resin (L.R. White™ Wirsam/London Resin Company). Sections were made with a Reichert-Jung Ultracut E microtome and contrasted with 2% uranyl acetate (pH 2) and lead citrate (Anala R). Sections were examined with a Philips CM10 Transmission Electron Microscope.

Pollen terminology follows Punt *et al.* (2007).

## RESULTS

Pollen grains of the southern African *Boerhavia* and *Commicarpus* species are spheroidal, pantoporate and the tectum is tubuliferous and spinulose. Spinules are (1.12–)2.70(–5.43)  $\mu\text{m}$  long and the pores are covered with a pore plate with one to two spinules (Figures 1, 2, 3). Exine is (3.35–)6.55(–11.45)  $\mu\text{m}$  thick. The tectum is (0.88–)2.09(–3.93)  $\mu\text{m}$  thick and tubuliferous, the collumellae are short [(0.64–)1.33(–2.82)  $\mu\text{m}$ ], the foot layer is (0.86–)2.67(–5.12)  $\mu\text{m}$  thick and the endexine is barely perceptible (Figure 4).

Pollen grains of the *Boerhavia* species are (51.59–)64.59(–91.48)  $\mu\text{m}$  diam.; the pores are (2.77–)4.46(–7.67)  $\mu\text{m}$  diam. and the exine (3.35–)6.99(–11.45)  $\mu\text{m}$  thick. The tectum is (0.88–)1.89(–3.78)  $\mu\text{m}$  thick and tubuliferous, the collumellae are short [(0.64–)1.32(–2.80)  $\mu\text{m}$ ], and the foot layer is (1.42–)2.98(–5.12)  $\mu\text{m}$  thick. Pollen grains of *B. deserticola* are the largest and those of *B. repens* subsp. *repens* the smallest (Table 1). Exine of the naturalised *B. diffusa* var. *diffusa* is the thickest (Table 1). *Boerhavia hereroensis* is the indigenous species with the thickest exine, while *B. repens* subsp. *repens* has the thinnest (Table 1).

Pollen grains of the *Commicarpus* species are (51.59–)79.80(–129.28)  $\mu\text{m}$  diam.; the pores are (2.59–)5.62(–10.64)  $\mu\text{m}$  diam. and the exine (4.05–)6.16(–9.10)

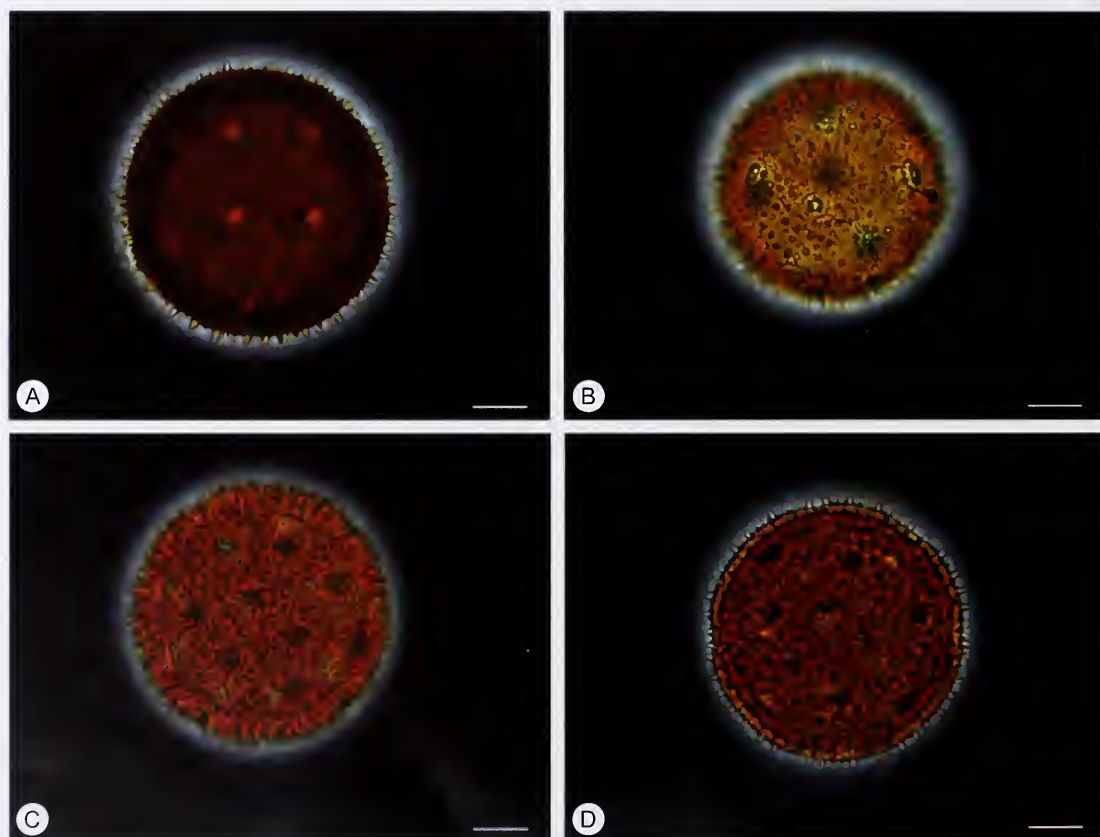


FIGURE 1.—Light micrographs of pollen grains of A, *Boerhavia deserticola* (Struwig 42); B, *B. hereroensis* (Struwig 34); C, *Commicarpus falacissimus* (Struwig 43); D, *C. squarrosus* (Struwig 41). Scale bars 20  $\mu\text{m}$ .

µm thick. The tectum is (1.19–)2.28(–3.93) µm thick and tubuliferous, the collumellae are short [(0.65–)1.34(–2.82) µm] and the foot layer is (0.86–)2.37(–3.82) µm thick. Pollen grains of *C. decipiens* are the largest and those of *C. helenae* var. *helenae* the smallest (Table 1). Exine of *C. pilosus* is the thickest and that of *C. helenae* var. *helenae* the thinnest (Table 1).

DISCUSSION

Pollen grain size range in the southern African species of *Boerhavia* is smaller than but overlapping the range reported by Nowicke (1970) for *Boerhavia* from the Americas (Table 1; Table 2). Nowicke (1970) studied *B. erecta*, which also occurs naturalised in southern

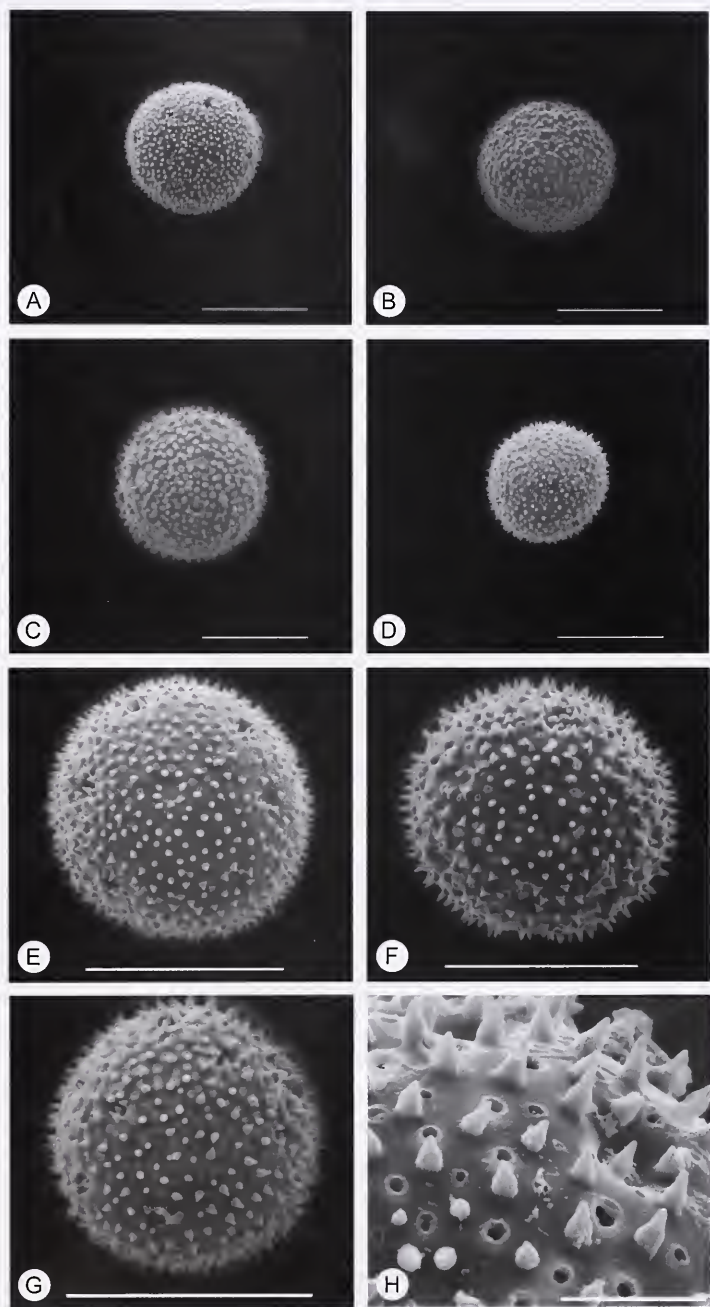


FIGURE 2.—Scanning electron micrographs of pollen grains of southern African *Boerhavia* species. A, *B. coccinea* var. *coccinea* (Struwig 55); B, *B. cordobensis* (Straub 499); C, *B. deserticola* (Struwig 42); D, *B. diffusa* var. *diffusa* (Struwig 88); E, *B. erecta* (Struwig 133); F, *B. hereroensis* (Struwig 34); G, *B. repens* subsp. *repens* (Acocks 21788); H, surface of a pollen grain of *B. deserticola* at higher magnification (Struwig 42). Scale bars A–G, 50 µm; H, 10 µm.



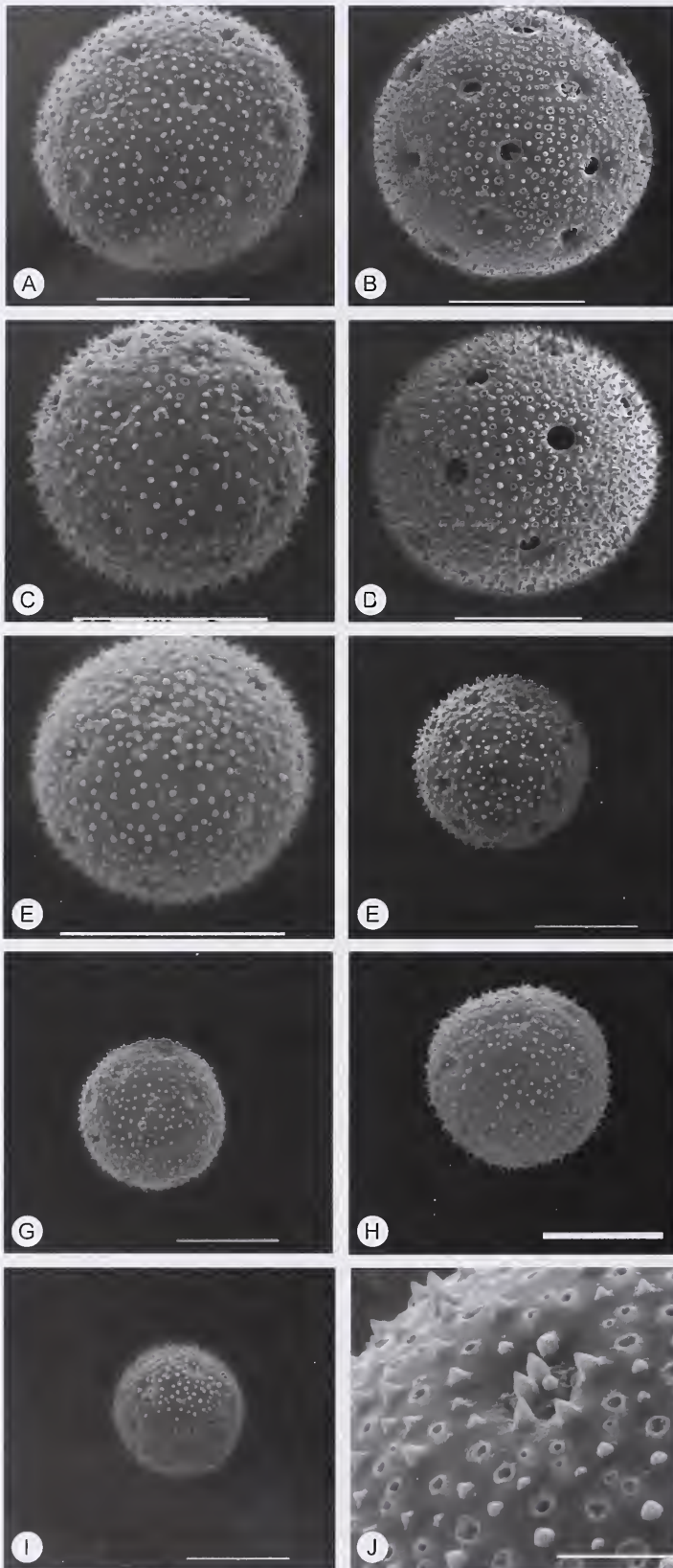


FIGURE 3.—Scanning electron micrographs of pollen grains of southern African *Commicarpus* species. A, *C. chinensis* subsp. *natalensis* (Struwig 63); B, *C. decipiens* (Struwig 181); C, *C. fallacissimus* (Struwig 46); D, *C. squarrosus* var. *fruticosus* (Struwig 160); E, *C. helenae* var. *helenae* (Struwig 44); F, *C. pentandrus* (Struwig 52); G, *C. pilosus* (Straub 609); H, *C. plumbagineus* var. *plumbagineus* (Struwig 106); I, *C. squarrosus* var. *squarrosus* (Struwig 41); J, surface of a pollen grain of *C. decipiens* at higher magnification (Struwig 181). Scale bars A, C, F–I, 50  $\mu$ m; B, 65  $\mu$ m; D, 35  $\mu$ m; J, 10  $\mu$ m; E, 20  $\mu$ m.



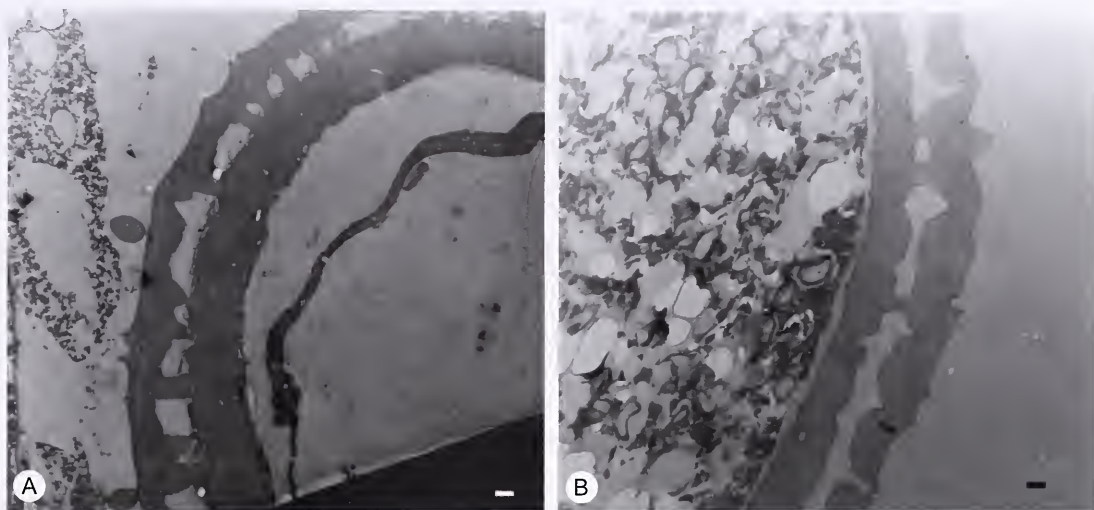


FIGURE 4.—Transmission electron micrographs showing the exine of portions of pollen grains of A, *Boerhavia deserticola* (Struwig 43); B, *Commicarpus decipiens* (Struwig 176). (C, columellae; E, endexine; F, foot layer; T, tectum). Scale bar 1  $\mu$ m.

Africa, and recorded the diameter of the grains to be nearly twice as large as that measured for the present study (Table 1; Table 2). The shape and sculpturing are, however, the same. Nowicke (1970) also studied three *Commicarpus* species, namely *C. brandegei* from Mexico, and *C. fruticosus* and *C. pentandrus* from southern Africa. The pollen shape and sculpturing of the latter two (Nowicke 1970) correspond with the findings of the present study, although the size range measurements of the grain diameters are less than that measured by Nowicke (1970) and the pore diameter is larger than that measured by Nowicke (1970) (Table 1; Table 2).

Perveen & Qaiser (2001) studied the pollen morphology of the Nyctaginaceae in Pakistan and included species also found in southern Africa, namely *B. diffusa* var. *diffusa*, *B. repens* subsp. *repens* and *C. helenae* var. *helenae*. The present study confirms the pollen shape and sculpturing of these three species given by Perveen & Qaiser (2001), but in some instances the diameter of the pollen grains, the pore diameter and the exine thickness differ. Slight differences in measurements between this study and that of Perveen & Qaiser (2001) can be ascribed to natural variation within the species and between geographical areas.

Pollen grain diameter of *B. repens* subsp. *repens* (Table 1) is substantially less than that reported by Perveen & Qaiser (2001) (Table 2). Pore diameters of *B. diffusa* var. *diffusa* and of *B. repens* subsp. *repens* (Table 1) show a slight overlap with the measurements of Perveen & Qaiser (2001) (Table 2). Exine of *B. diffusa* var. *diffusa* (Table 1) is significantly thicker than reported by Perveen & Qaiser (2001) (Table 2).-

The columellae of the studied species are short, the foot layer is thick and the endexine is barely perceivable (Table 1). This is consistent with palynological studies on members of the Nyctaginaceae by Skvarla & Nowicke (1976) and Nowicke & Skvarla (1979), involving *Salpianthus arenarius* Humb. & Bonpl., *Pisonia aculeata* L. and *B. erecta*. Skvarla & Nowicke (1976)

specifically noted that the endexine of *Boerhavia* is barely perceptible.

Pollen morphology (shape and sculpturing) of *Boerhavia* and *Commicarpus* is not diagnostic, and although pollen grains of the *Boerhavia* species are smaller than those of the *Commicarpus* species (Table 1), the ranges overlap substantially, making it impossible to distinguish between the genera with the aid of numerical measurements alone. Pore diameter of *Commicarpus* species has a higher range than that of *Boerhavia* species and the exine of *Commicarpus* species has a lower range in thickness than that of *Boerhavia* species (Table 1). However, the overlap in size ranges of the pollen grains, pore diameter and thickness of the exine does not provide sufficient discontinuity to distinguish between the two genera, nor the individual species.

#### CONCLUSION

The pollen morphology of ten southern African species of *Boerhavia* and *Commicarpus* was described for the first time and proved to be essentially uniform in shape and sculpturing. Pollen grains are spheroidal and pantoporate and the tectum is tubuliferous and spinulose. Pollen grains of *Boerhavia* are generally smaller than those of *Commicarpus* species. Pore diameter in *Commicarpus* is generally larger than that in *Boerhavia* and the exine in *Commicarpus* is thinner than in *Boerhavia*. However, the use of grain dimensions to distinguish among taxa is unreliable due to the extensive overlap in size ranges.

Although pollen morphology distinguishes broadly between the genera, the shape and size of the pollen grains show too much variation within species to be useful for distinguishing between species. Therefore, this southern African study confirms earlier reports that palynological characters are of limited taxonomic value in distinguishing between *Boerhavia* and *Commicarpus* and their species.

Table 1.—Measurements of pollen grains of *Boerhavia* and *Commicarpus* species

Taxon	Diameter of grains (µm)	Diameter of pores (µm)	Length of spinules (µm)	Thickness of spinules (µm)	Thickness of exine (µm)	Thickness of the tectum (µm)	Length of the col-lumella (µm)	Thickness of the footlayer (µm)
<i>Boerhavia coccinea</i> var. <i>coccinea</i>	(53.08–) 66.48 (–91.48)	(3.48–) 4.44 (–5.97)	(1.72–) 2.61 (–3.75)	(6.30–) 6.70 (–7.74)	(1.59–) 2.37 (–3.33)	(0.64–) 1.06 (–1.53)	(2.33–) 3.66 (–5.27)	
<i>Boerhavia cordobensis</i>	(56.34–) 66.59 (–80.65)	(3.38–) 4.08 (–4.71)	(1.77–) 2.71 (–3.61)	(6.50–) 7.02 (–7.46)	(1.39–) 2.50 (–3.78)	(0.98–) 1.23 (–1.69)	(2.53–) 3.30 (–4.25)	
<i>Boerhavia deserticola</i>	(65.42–) 74.55 (–82.54)	(4.67–) 5.34 (–6.12)	(1.83–) 3.58 (–5.43)	(4.48–) 6.58 (–8.10)	(1.01–) 1.79 (–2.82)	(0.67–) 1.52 (–2.38)	(1.42–) 2.12 (–3.10)	
<i>Boerhavia diffusa</i> var. <i>diffusa</i>	(51.99–) 63.26 (–76.19)	(3.13–) 4.31 (–4.73)	(1.82–) 3.04 (–3.84)	(7.75–) 8.78 (–9.69)	(1.17–) 1.54 (–1.81)	(0.86–) 1.23 (–1.49)	(3.02–) 3.90 (–5.12)	
<i>Boerhavia erecta</i>	(57.09–) 64.15 (–69.15)	(3.08–) 4.23 (–4.59)	(1.83–) 2.16 (–2.86)	(4.76–) 6.81 (–10.22)	(1.15–) 1.59 (–2.25)	(1.06–) 1.38 (–1.72)	(1.15–) 1.59 (–2.25)	
<i>Boerhavia hereroensis</i>	(49.06–) 60.77 (–74.62)	(3.30–) 4.79 (–7.67)	(1.47–) 2.70 (–4.01)	(5.64–) 8.57 (–11.45)	(1.66–) 1.98 (–2.45)	(0.98–) 1.67 (–2.80)	(2.13–) 3.00 (–4.45)	
<i>Boerhavia repens</i> subsp. <i>repens</i>	(45.07–) 57.89 (–68.25)	(2.77–) 4.03 (–5.41)	(2.03–) 3.05 (–3.98)	(3.35–) 4.02 (–4.96)	(0.88–) 1.19 (–1.93)	(0.64–) 1.03 (–1.55)	(1.67–) 2.08 (–2.43)	
<i>Commicarpus chinensis</i> subsp. <i>natalensis</i>	(70.26–) 97.04 (–121.04)	(3.40–) 5.46 (–7.37)	(1.78–) 2.76 (–3.43)	(4.13–) 5.30 (–6.71)	(1.19–) 2.00 (–2.82)	(0.75–) 1.56 (–2.16)	(1.39–) 2.00 (–2.60)	
<i>Commicarpus decipiens</i>	(97.40–) 116.64 (–129.28)	(4.81–) 5.03 (–5.37)	(1.45–) 2.43 (–3.01)	(5.79–) 7.35 (–9.10)	(2.35–) 2.84 (–3.35)	(1.39–) 1.7 (–2.82)	(1.45–) 2.78 (–3.82)	
<i>Commicarpus fallacissimus</i>	(63.88–) 76.62 (–88.46)	(4.35–) 5.25 (–5.92)	(2.18–) 3.18 (–3.78)	(4.76–) 4.81 (–4.93)	(1.21–) 1.49 (–1.86)	(0.81–) 1.21 (–1.42)	(1.4–) 1.59 (–1.87)	
<i>Commicarpus helenae</i> var. <i>helenae</i>	(53.76–) 60.60 (–71.29)	(2.59–) 4.35 (–5.00)	(1.12–) 1.72 (–1.87)	(3.57–) 4.26 (–5.11)	(1.05–) 1.73 (–2.67)	(1.01–) 0.95 (–1.07)	(0.86–) 1.51 (–1.86)	
<i>Commicarpus penandrus</i>	(63.74–) 84.23 (–100.12)	(3.47–) 5.76 (–8.45)	(2.39–) 3.36 (–4.84)	(4.65–) 6.40 (–8.28)	(1.45–) 2.55 (–3.20)	(0.65–) 1.25 (–1.66)	(1.60–) 2.39 (–2.84)	
<i>Commicarpus pilosus</i>	(67.55–) 71.97 (–77.66)	(4.55–) 5.04 (–5.49)	(1.88–) 2.55 (–3.26)	(6.69–) 7.45 (–9.06)	(1.48–) 2.00 (–3.11)	(0.78–) 1.20 (–1.92)	(2.20–) 2.66 (–3.53)	
<i>Commicarpus plumbagineus</i>	(71.99–) 85.26 (–105.27)	(3.70–) 5.82 (–8.30)	(1.19–) 1.95 (–2.77)	(4.93–) 6.02 (–6.99)	(2.36) 2.4 (2.52)	(1.59–) 1.76 (–2.03)	(2.05–) 2.53 (–3.09)	
<i>Commicarpus squarrosus</i> var. <i>fruticosus</i>	(64.64–) 76.23 (–87.89)	(4.36–) 7.11 (–10.64)	(1.95–) 2.49 (–4.02)	5.00	(2.03–) 2.79 (–3.93)	(0.97–) 1.26 (–1.76)	(2.73–) 3.08 (–3.97)	
<i>Commicarpus squarrosus</i> var. <i>squarrosus</i>	(45.55–) 65.49 (–82.54)	(3.30–) 4.77 (–6.12)	(1.47–) 2.89 (–5.43)	(3.88–) 5.23 (–6.16)	(1.19) 1.77 (2.43)	(0.78–) 1.13 (–1.39)	(1.09–) 1.76 (–2.30)	

Table 2.—Measurements made of *Boerhavia* and *Commicarpus* pollen grains by <sup>a</sup>Nowicke (1970) and <sup>b</sup>Perveen & Qaiser (2001)

Taxon	Diameter of grains (µm)	Diameter of pores (µm)	Length of spinules (µm)	Thickness of the nexine (µm)	Thickness of the sexine (µm)	Thickness of the exine (µm)
<sup>a</sup> <i>Boerhavia</i>	70–138	2.4–7	1–5	4–7	2.5–6	-
<sup>b</sup> <i>B. diffusa</i> var. <i>diffusa</i>	50–62.5	2.5–7.5	4.25–5.25	-	-	2.22–3.33
<sup>a</sup> <i>B. erecta</i>	121–138	6–7	4–5	5–5.5	2.5–3	-
<sup>b</sup> <i>B. repens</i> subsp. <i>repens</i>	61.03–100.5	3.23–3.94	3.59–7.18)	-	-	3.23–3.59
<sup>a</sup> <i>Commicarpus</i>	84–112	3–5.5	1–2.5	2.5–5.5	2.5–5.5	-
<sup>a</sup> <i>Commicarpus fruticosus</i>	84–92	3–4	2–2.5	2.5–3	2.5	-
<sup>b</sup> <i>C. helenae</i> var. <i>helenae</i>	50–60	2.5–5.1	3.75–5.01	-	-	1.11–2.22
<sup>a</sup> <i>Commicarpus pentandrus</i>	98–110	4.5–5.5	2–2.5	4.5–5	4	-

<sup>a</sup>*Commicarpus fruticosus* syn. of *C. squarrosus* var. *fruticosus*

Specimens examined

NAMIBIA.—1813 (Opuwo): Joubert Pass to Opuwo, against slope in stony/rocky soil, (–DD), 9 Feb. 2009, *Struwig 46* (PUC, WIND). 1913 (Sesfontein): Khowarib Rest Camp, behind the tents underneath acacia and mopane trees, (–BD), 9 Feb. 2009, *Struwig 44* (PUC, WIND); on road to Sesfontein, next to road in dry stream bank, (–DB), 8 Mar. 2009, *Struwig 43* (PUC, WIND). 1917 (Tsumeb): Tsumeb, at junction of D3022 and D2863, Otavi mountains, (–BD), 10 Feb. 2009, *Struwig 48* (PUC, WIND). 2014 (Khorixas): Twyfelfontein Lodge, hills behind lodge, SW of main building (–CB), 7 Feb. 2009, *Struwig 40, 41* (PUC, WIND); Twyfelfontein, village near Twyfelfontein Lodge, in dry streambed, (–CB), 8 Feb. 2009, *Struwig 42* (PUC, WIND). 2016 (Otjiwarongo): Otjiwarongo, Gobabis road, corner of C30 and C22, (–DB), 11 Feb. 2009, *Struwig 52* (PUC, WIND). 2017 (Waterberg): Otjiwarongo, Klein Waterberg, at foot of mountain in shade of trees, (–CA), 11 Apr. 2010, *Struwig 181* (PUC, WIND). 2114 (Uis): Uis, Brandberg, near entrance to Tsisab gorge, (–AA), 6 Feb. 2009, *Struwig 38* (PUC, WIND). 2115 (Trekopje): Omaruru, Loskop farm, (–BD), 11 Apr. 2010, *Struwig 176* (PUC, WIND); Usakos, Klein Spitzkuppe, against mountain slope amongst rocks, (–CC), 5 Feb. 2009, *Struwig 35, 36* (PUC, WIND); Karibib, Klippenberg Country Club, rocky hill behind restaurant, (–DD), 4 Feb. 2009, *Struwig 34* (PUC, WIND). 2116 (Okahandja): Okahandja, D2110, first dry stream bank after entrance to farm Okatjiho, (–DD), 12 Feb. 2009, *Struwig 54, 55* (PUC, WIND). 2217 (Windhoek): Windhoek National Botanical Garden, Lily Walk, (–CA), 3 Feb. 2009, *Struwig 33* (PUC, WIND); D1463, at T-junction sign just before entrance to Aris Farm, (–CC), 13 Feb. 2009, *Struwig 57* (PUC, WIND). 2416 (Maltahöhe): C 14, Naukluft Mtns, mountain slope behind the river, (–AA), 13 Feb. 2009, 7 Apr. 2010, 8 Apr. 2010, *Struwig 160, 163* (PUC, PRE, WIND); C19, Tsaris Mtns, (–AB), 8 Apr. 2010, *Struwig 164* (PUC, WIND); Maltahöhe, D850, next to road, (–DB), 9 Apr. 2010, *Struwig 168* (PUC, WIND).

LIMPOPO.—2229 (Waterpoort): Mapungubwe National Park, Rhodesdrift, garden of Section Ranger, (–AA), 18 Nov. 2009, *Struwig 117* (PRE, PUC); Pont Drift, Breslau 2MS, dam wall area, (–AC), 28 Jul. 1998, *Straub 499* (PRE); Pont Drift, Breslau 2MS, NE base of Pyramid koppie, (–AC), 14 May 1997, *Straub 609* (PRE); On Waterpoort–Alldays road, (–CD), 17 Nov. 2009, *Struwig 111* (PRE, PUC); 9 km on Waterpoort–Alldays road, (–DC), 17 Nov. 2009, *Struwig 110* (PRE, PUC); Louis Trichardt (Makhado), just after tunnel coming from Louis Trichardt on farm Klein Afrika, on riverbank, (–DD), 17 Nov. 2009, *Struwig 106* (PUC, PRE). 2230 (Messina): R525, 4 km after Tspise, (–CA), 19 Nov. 2009, *Struwig 122* (PRE, PUC);

NORTH-WEST.—2626 (Klerksdorp): Klerksdorp, Doringkruin, pavement on the corner of Moepel Avenue and Oleander Avenue, (–DC), 16 Jan. 2010, *Struwig 132* (PRE, PUC). 2627 (Potchefstroom): Potchefstroom, N12 Johannesburg road at Alpha Fruit and Veggies, Plot 283, next to road, (–CA), 4 Dec. 2008, *Struwig 23* (PRE, PUC); Potchefstroom, Bailliepark, 108 Steyn Street, (–CA), 2 Feb. 2010, *Struwig 133* (PRE, PUC).

MPUMALANGA.—2431 (Acornhoek): Kruger National Park, H4-1 from Skukuza to Nkuhlu, along Sabie River, (–DC), 21 Apr. 2009, *Siebert 3970* (PUC); Kruger National Park, in Skukuza Research Camp, behind tents and bungalows underneath trees, (–DC), 16 Mar. 2010, *Struwig 143* (KNP, PUC).

KWAZULU-NATAL.—2831 (Nkandla): Richards Bay, Mtuzini Nature Reserve, next to road opposite entrance to Inkwazi Campsite, (–DD), 12 Mar. 2009, *Struwig 88* (NH, PUC). 2832 (Mtubatuba): Richards Bay, Naval Hill, (–CC), 12 Mar. 2009, *Struwig 62* (PUC, NH); Richards Bay, Richards Bay Camping Site, Block E & F, in vegetation forming borders around campsites, (–CC), 12 Mar. 2009, *Struwig 63* (PUC, NH). 2931 (Stanger): Umhlanga Rocks, trail past the bridge going over the lagoon, against dune slope facing the beach, (–CA), 10 Mar. 2009, *Struwig 61* (NH, PUC).

NORTHERN CAPE.—2824 (Kimberley): Hay division, 11 Mar. 1937, *Acocks 1978* (KMG, PRE). 2921 (Kenhardt): Kenhardt division, 25.8 miles SW by W of Kenhardt, (–AC), 4 Feb. 1961, *Acocks 21788* (PRE).

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# Reproductive biology of *Stomatium bolusiae* (Aizoaceae: Ruschioideae)

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**Keywords:** Aizoaceae, crepuscular, melittophily, phalaenophily, pollination, Ruschioideae, seed germination, *Stomatium* Schwantes

## ABSTRACT

Flowers of *Stomatium bolusiae* are self-incompatible. The species exhibits crepuscular and nocturnal anthesis, exploiting two different pollination mechanisms. The structure of the hermaphroditic flower appears not to favour cross-pollination. The stigmata are never exposed to pollinating agents, which gain access to the floral rewards by forcing their way between the anthers. Clogging of the stigmatic surfaces by self-pollen is common. Nocturnal anthesis, concomitant with the nocturnal release of attractants and the offering of rewards, indicates that this species is primarily phalaenophilous and secondarily melittophilous, exhibiting a bimodal pollination system.

## INTRODUCTION

Few data exist on the pollination biology or related aspects of Aizoaceae subfamilies Mesembryanthemoideae and Ruschioideae, commonly referred to as mesembs (Vogel 1954; Liede & Hammer 1990; Liede *et al.* 1991; Struck 1995; Hammer 2002; Hartmann 1991, 2002a, 2002b; Juergens 2004; Peter *et al.* 2004; Thiede *et al.* 2011). The only studies in South Africa on visits and possible pollination of mesemb flowers by masarid wasps was conducted by Gess & Gess (1989) and Struck (1994). In diurnal flowering species, the prominence of the bright shiny petals and the open pollen presentation suggest that insects pollinate these flowers (Hartmann 1991).

Available information on anthesis in mesembs is based on studies by Hartmann (1978, 1991) and Hartmann & Dehn (1987), who observed that flowers opening during the day are protandrous, with a very distinctive early male phase, followed by a later female phase. The flowers open repeatedly by basal growth of the androecial elements (Hartmann 1978, 1991). In melittophilous flowers the stigmas are at first shorter than the stamens. During the female phase, the stamens wither and collapse and the elongated stigmas are prominently displayed in the middle of the flower. At this stage the stigmas spread and start to produce a copiously papillate surface, which is more intensively coloured than in the unripe stage. The genus *Stomatium* is regarded as having melittophilous flowers of the recess type (Hartmann 1978, 1991).

Vogel (1954) suggested that visiting insects crawl into this hidden cavity, the depth and width of which may vary between species, in order to reach nectar or pollen. During this activity, pollen is deposited all over the body of the insect.

*Stomatium* Schwantes is one of numerous genera of Aizoaceae subfam. Ruschioideae (Bittrich & Hartmann 1988; Hartmann 1991). *Stomatium* species are widely

distributed through the drier parts of the Western, Northern and Eastern Cape and the central Free State (Smith *et al.* 1998). The genus *Stomatium* comprises 39 species (Smith *et al.* 1998) of which only *S. bolusiae* occurs in the Free State (Chesselet *et al.* 2003). The plants are generally found on rocky outcrops in very shallow soil. The leaves are olive green to drab-grey during favourable periods but take on a reddish or purple colour when stressed, thus blending with the surrounding environment (Smith *et al.* 1998).

The aim of this study was to describe the pollination biology of *S. bolusiae* under natural conditions.

## MATERIALS AND METHODS

### *Study area*

The research was conducted in natural veld in an undisturbed part of the Free State National Botanical Garden (2926AA). *S. bolusiae* occurs abundantly on the dolerite outcrops around Bloemfontein. It grows in shallow, gravel-filled depressions and cracks on these outcrops and, during the summer, is exposed to prolonged wet periods after good rains and to drought conditions with extremely high temperatures in between. The vegetation of this area forms part of the Bloemfontein Karroid Shrubland (Gh 8) (Mucina & Rutherford 2006).

### *Pollen-ovule ratio and pollen viability*

Pollen grains were collected from 10 anthers from each of five different flowers representing different ages during the life span of the flowers. These were then separately suspended in 10 ml of a 0.1% (m/v) aniline blue staining solution. After the solutions were thoroughly shaken, pollen grains from four samples of each solution were counted using a haemocytometer. The mean of these four replicates was taken to represent the number of pollen grains per anther. This was then used to determine the standing crop of pollen grains per flower.

Since the ovules are very soft and extremely difficult to dissect from the ovary, seeds of mature fruits were counted and the highest observed value from the ten different mature cross-pollinated capsules, previously unexposed to rain, and excluding the possibility of seed

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loss, was used. This value, together with the average number of pollen grains, was used to obtain an estimate of the pollen/ovule (P/O) ratio. These calculations are based on flowers collected during the 1998/1999 season.

Pollen viability was determined by examining a mixed pollen sample, consisting of pollen from 10 different flowers, using Alexander's viability stain (Alexander 1969) and by means of the fluorochromatic (FCR) test procedure (Heslop-Harrison *et al.* 1984).

#### *Floral behaviour*

Ten different individual flowers were monitored for eight days between 16:30 in the afternoon until 04:00 the following morning: (a) to determine the reproductive viable period of flowers from the onset of anthesis and (b) to describe floral behaviour. Observations were recorded at 30-minute intervals. Movement of calyx lobes, petals and anthers were noted. Changes in secretion of nectar glands were also noted.

To test for floral fragrance, different flowers representing the seven days during the life span of the flowers were collected shortly after opening. For each of these days, five flowers were kept in closed vials for a period of three hours. On opening the vials, the odour was evaluated on a subjective scale of 0 (odour absent) to 3 (strong odour) by three different persons. Thereafter, flowers were dissected and the same experiment was conducted on the calyx lobes, pistils, petals and stamen. To localise osmophores, the floral parts were stained with a 0.1% (m/v) neutral red solution for  $\pm$  five hours (Van Wyk & Lowrey 1988). The presence and availability of nectar and pollen were noted during anthesis.

#### *Pollination experiments and seed set*

Experiments were conducted on a single intact flower per plant. A total of 50 flowers were used for each experiment. For microscopic work these flowers were collected 24 hours after having been artificially pollinated and fixed in Carnoy's solution (Samaha *et al.* 1989). Experiments were conducted as described by Bawa (1974), Gunatilleke & Gunatilleke (1984) and Harvey & Braggins (1985). Pollen tube growth and germination were determined *in vivo* by a technique based upon the fluorescence of callose (Martin 1959; Jefferies & Brain 1984). Pistils were destained with Gillett's Javel commercial bleach containing 3.5% (m/v) sodium hypochlorite, after which the material was thoroughly rinsed in distilled water. After staining with decolourised aniline blue, pollen germination and pollen tube growth were observed using a Zeiss Axioskop equipped with a 100 W high pressure Hg lamp and filter set for UV light excitation. Apomixis was not considered during these experiments as the required emasculatation would have damaged the flowers. No flowers were therefore emasculated.

#### *Pollination treatments*

Open pollination: flowers were marked and left to test for fruit and seed set.

Autogamy: plants were bagged and left without any manipulation to test for selfing. Due to the leaves covering the fairly short flower stalk and the possibility of

damaging the flowers and influencing the experiment, individual flowers were not bagged. Chiffon (a light-weight, balanced, plain-woven sheer fabric) with a mesh size of  $250\mu\text{m} \times 250\mu\text{m}$  was loosely stretched over the plant, allowing enough room for floral movement but excluding possible pollinators. It was anchored to the soil with pins. Care was taken to avoid any damage to the plant. Bagging was done in the same way throughout the experiment.

Self-compatibility: flowers were self-pollinated by hand.

Geitonogamy: pollen from one flower was used to pollinate the stigma from another flower on the same plant.

Xenogamy: flowers were crossed with pollen collected from plants 10 m or more from the ones used for the experiment (Waser & Price 1983).

Evaluation of fruit and seed set is based on counts made one month after marking the individual flowers. As it was not clear how many ovules normally abort in the ovaries, an *index of seed set* was used. This was calculated by dividing the actual number of seeds in any capsule by the maximum number of seeds that could be expected to develop under ideal conditions. The latter value represented the highest number of seeds counted in cross-pollinated flowers. Since seed dispersal in *Stomatium* species is initiated by the opening of dry capsules during rain (ombrohydrochory), the risk of losing seeds had to be minimised. Dry capsules, which had not been exposed to rain before, were therefore collected and their seeds counted.

#### *Pollinator behaviour; attractants and rewards*

The behavioural pattern of insect visitors to the flowers was observed over a period of five days and nights. Thereafter visitors were collected, killed in 100% ethyl acetate, identified and examined for the presence of *Stomatium* pollen. The placement of pollen on their bodies was noted. Visiting pollinators were identified, counted and visitation rates expressed as number of insects per plant per hour.

#### *Fruit and seed set*

To determine the success of seed set throughout the year, 50 mature flowers were marked with threads of cotton every month between September 2001 and August 2002. Ripe capsules were collected  $\pm$  three to four weeks after being tagged. In total 600 mature capsules were marked and collected during this period. The number of seeds per capsule was determined for each month and compared with the rainfall figures for the same period.

## RESULTS

#### *Floral behaviour*

The flowers have short stalks and numerous, bright yellow petals. Flowering starts in early spring during August and continues until early winter at the end of May. Plants very seldom flower in mid-winter. During early spring, flowers open only after relatively warm,



sunny days but not on cold and/or overcast afternoons or evenings. Between late August and the end of September, anthesis is crepuscular, occurring at dusk ( $\pm 20$  min before sunset at 18:00). Later in the season, October to April, anthesis is nocturnal, taking place only after sunset. Flowers close well before sunrise at about 04:00. Most flowers last up to seven (eight in some individuals) days. There is variation between the timing of presentation between the male and female phases in the population. In some individuals there is almost complete overlap of pollen presentation and stigma receptivity, while in others dehiscence of the anthers starts one hour before the stigmas become receptive. On the first evening, at the onset of anthesis, the five stigmas are dry and clearly distinguishable and stigmatic papillae are clearly visible. Stigmatic secretion, anther dehiscence and nectar production start within one hour after the onset of anthesis.

A strong sweet odour is emitted by the flowers during the first four evenings (Figure 1) but becomes almost undetectable from the fifth night. Osmophores could not be detected when staining with neutral red. No odour could be perceived during daytime.

Nectar and pollen are available from the start of anthesis until day five. At the start of the second

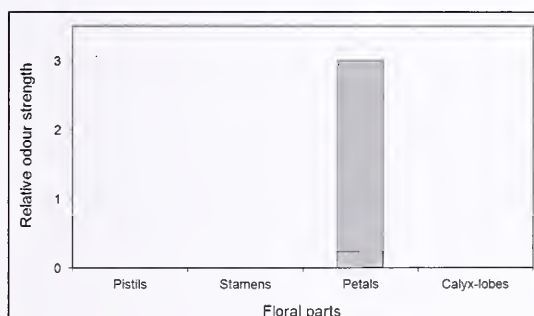


FIGURE 1.—Contribution to odour release by different floral parts of *Stomatium bolusiae*.

evening, the stigmas are already clogged and indistinguishable from each other as a result of prolific stigmatic secretion. Pollen is still available and the odour is still strong (Figure 2). At this stage the sticky pollen is available in large quantities and easily noticeable. On the fifth evening, odour and nectar production stop. At this stage noticeably fewer pollen grains are left in the anthers. At the end of night seven, the calyx lobes fail to fold back to their original position, indicating the end of anthesis. Depending on the longevity of a specific flower, the reproductive period appears to be between days one and five (occasionally six).

The average number of pollen grains is 274 314 per flower. The highest number of seeds observed in mature cross-pollinated capsules was 262. The pollen-ovule ratio of *S. bolusiae* is therefore estimated to be 1 047:1. Staining with Alexander's stain indicated that 94% of the pollen grains were potentially viable whereas the FCR test procedure indicated that only 75% of the pollen grains with live protoplast were germinable.

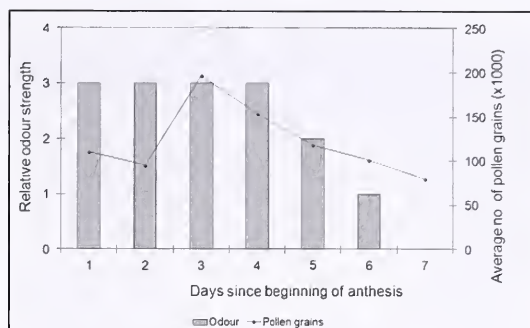


FIGURE 2.—Relative odour strength and availability of pollen grains during life span of flowers of *Stomatium bolusiae*. Shaded area, odour; graph, pollen grains.

### Pollination experiments

Fruits were formed in 91% of the flowers that were marked to test for natural fruit set (open pollination) during September and October 1998/99. The index of seed set in these fruits was 58.4% and 75% in cross-pollinated flowers (xenogamy). In self-pollinated flowers, pollen grains germinated but pollen tube growth was arrested in the style and none of these flowers set seed (Figure 3A, B). None of the flowers that were tested for geitonogamy set seed.

### Pollinator behaviour, attractants and rewards

Honeybees, *Apis mellifera* (Hymenoptera: Anthophoridae) visit the open flowers during early dusk. They approach the flowers from downwind and alight on top of the flowers. As the recess inside the flower is too small for the bees to get into, they force their heads into the flower to collect nectar and pollen, touching the petals and anthers. During this action, they come into contact with the pollen and stigmas. Once they have started collecting the available rewards they do not move around on the flower. Pollen was found on the heads, thorax and mouth parts of the bees. The only other visitors of significance are nocturnal moths (*Spodoptera* sp., Lepidoptera: Noctuidae), which visited the flowers throughout the flowering season. Pollen was found on the proboscises of these moths. As with honeybees, moths approach the flowers from downwind, land directly on top of an open flower and collect nectar by pushing their proboscis into the recess of the flower. They do not force their bodies into the flower. Visitation rates of bees (15/plant/hour) were higher than that of moths (0.8/plant/hour). No ants were observed visiting the flowers.

### Fruit and seed set

All capsules marked during September 2001 and February 2002 matured. The most unsuccessful period for fruit set was during November and December 2001 when only 68% and 56% capsules ripened (Figure 4). The highest seed set was achieved during early summer (September and October 2001) and late autumn (May 2002). The highest number of seeds was produced during October 2001 (122 seeds per capsule, 58% capsules ripened). The lowest seed set was recorded during

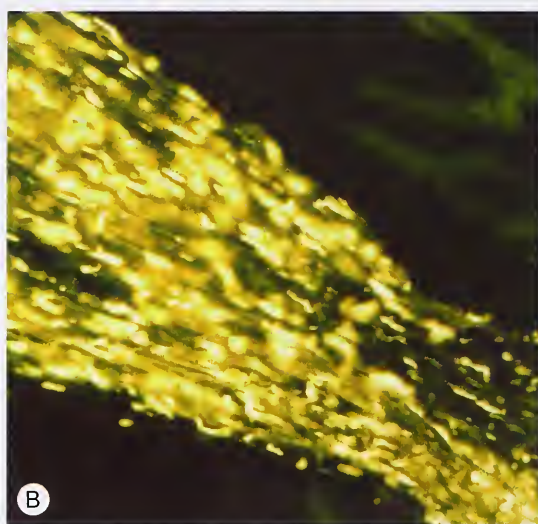
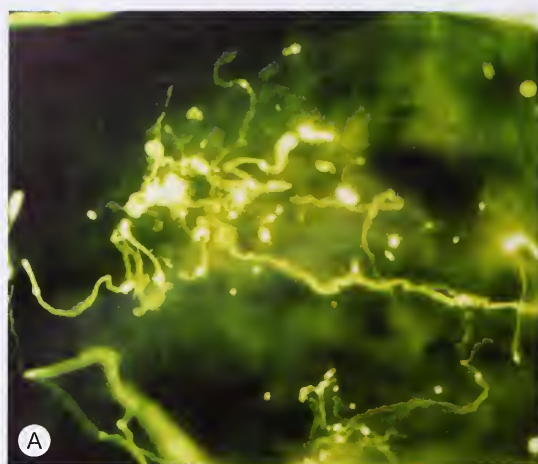


FIGURE 3.—Fluorescent micrograph of pollen tube growth in stigma and style of *Stomatium bolusiae* after staining with decolourised aniline blue: A, pollen tube growth of self-pollinated flowers arrested in style ( $\times 72$ ); B, normal growth in a cross-pollinated flower ( $\times 18$ ).

November and December 2001 and January 2002 when on average less than three seeds per capsule were produced. Flowering did not take place during midwinter (June/July) and no fruits or seeds were produced.

#### DISCUSSION

*Stomatium bolusiae* flowers are hermaphroditic and only bisexual flowers are borne. The life span of the flowers is seven days. In some flowers there is almost complete overlap of pollen presentation and stigma receptivity, as dehiscence of the anthers starts one hour before the stigmas become receptive in the majority of flowers. In others, this time lapse was not more than a few minutes and in some the male and female functions were not separated and overlapped completely. Furthermore, most individual plants have more than two receptive flowers, representing different days during its life span, at any one time. There is no clear separation (tem-

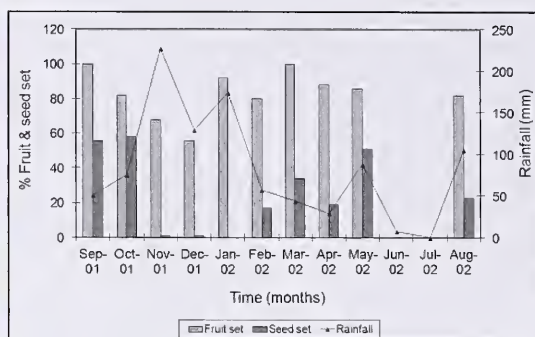


FIGURE 4.—Correlation of fruit and seed set of *Stomatium bolusiae* from September 2001 to August 2002, with rainfall received during same period. Pale shaded area, fruit set; dark shaded area, seed set; graph, rainfall.

poral or spatial) of male and female functions throughout anthesis. Flowers of *S. bolusiae* can therefore not be regarded as protandrous as described for most melitophilous flowers by Hartmann (1991), therefore floral behaviour indicates homogamy. Furthermore, the wet receptive surfaces of the papillate stigmas as well as the arresting of pollen tube growth in the short style and not on the stigmas, suggest gametophytic self-incompatibility (Heslop-Harrison & Shivanna 1977).

Although the petals have been indicated as the source of the flower fragrance, the source could not be determined by staining. The P/O ratio as used by Cruden (1977) indicates that *S. bolusiae* is a facultative xenogamous species. Dafni (1992) regards this ratio as a reflection of the breeding system but cautions that each case should be studied in relation to its specific pollination syndrome. Dafni (1992) furthermore sets the standards for evaluating breeding systems based on the P/O ratio at the family level and not at the species level. Currently not enough data/information exists for the mesemb. More studies should thus be conducted before any such conclusions can be drawn relevant to the family. Results obtained from pollination experiments showed that none of the pollen tubes in self-pollinated flowers grew the length of the style and that none of the flowers, thus treated, set seed. This confirms self-incompatibility. Despite the simultaneous presentation of male and female functions and severe clogging of the stigmas by self-pollen, *S. bolusiae* should not be regarded as a facultative but as an *obligate* xenogamous species.

Seed set resulting from cross-pollinated flowers (75%), in comparison to natural seed set of 58.4%, indicates an effective pollination mechanism. The flowers are obviously not adapted for a specialist pollinator. The highly specific anthesis time excludes visits from all but two species, resulting in a very specific pollination mechanism. Flowers earlier in the season exhibit crepuscular anthesis, at which time they are pollinated by honeybees, a very common pollinator. Bees are part of a generalist pollination system, visiting a wide range of flowers and are thus polylectic. They are involved as the main pollen vectors in a number of pollination studies conducted in the Free State (Zietsman 1990, 1991, 1993, 1994, 1998). These studies all demonstrated the



sharp decline in pollinator visits in the late afternoon. Since no other plants were in flower in the proximity of the *Stomatium* population, the crepuscular activity of the bees during the early part of the daily opening of the flower is perhaps a result of food scarcity. The only visitors encountered during the night were noctuid moths. Nocturnal anthesis, anther dehiscence, nectar secretion and fragrance production in this species is consistent with adaptation for nocturnal moth pollination. Most of these features are also consistent with bee pollination. *S. bolusiae* must therefore be regarded as a melitto- and phalaenophilous species exhibiting a bimodal pollination system (Manning & Goldblatt 2005).

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# A revised infrageneric classification and synopsis of the Afro-Eurasian genus *Moraea* (Iridaceae: Irideae)

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**Keywords:** Iridaceae, Iridoideae, *Moraea* Mill., new species, southern Africa, taxonomy

## ABSTRACT

Molecular phylogenetic studies of *Moraea* Mill. and the inclusion of *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandris* Parl., *Hexaglottis* Vent., *Homeria* Vent. and *Roggeveldia* Goldblatt in the genus have rendered the existing infrageneric classification, dating from 1976, in need of substantial revision. In particular, subg. *Moraea* and subg. *Vieusseuxia* have been shown to be paraphyletic. We propose a new infrageneric classification, based, as far as current data permit, on phylogenetic principles. Monophyletic subgenera and sections are circumscribed based on molecular phylogenies alone or in combination with morphological considerations. We recognize 11 subgenera, 15 sections and three series, arranged as follows in phylogenetic sequence: **Plumarieae**; **Visciramosae** (with sect. **Multifoliae** and sect. **Visciramosae**); *Moraea* (with sect. *Moraea* and sect. **Polyphyllae**); *Galaxia* (with ser. **Unguiculatae**, ser. *Eurystigma* and ser. *Galaxia*); **Monocephalae**; **Acaules**; **Polyanthes** (with sect. **Serpentinae**, sect. *Deserticola*, sect. *Hexaglottis*, sect. *Gynandris*, sect. *Polyanthes* and sect. **Pseudopicatae**); **Grandiflorae**; **Vieusseuxia** (with sect. **Integres**, sect. *Vieusseuxia* and sect. **Villosae**); and **Homeria** (with sect. **Stipanthera**, sect. *Flexuosae*, sect. *Homeria* and sect. **Conantherae**). Most are moderately to well circumscribed at the morphological level either by floral or vegetative characters, except subg. *Moraea*, which includes a small number of unspecialized species apparently not linked by any apomorphic features. With over 27 new species described in the past 25 years and another 60 transferred to the genus, *Moraea* now includes 214 species. We provide a full taxonomic synopsis of the genus.

## INTRODUCTION

*Moraea* Mill., the largest African genus of Iridaceae tribe Irideae, comprises ± 220 species (214 recognized species plus several more yet to be described). Following revisions of its southern and tropical African members (Goldblatt 1973, 1976a, 1977b), *Moraea* was believed to be well understood and was considered to be monophyletic, largely on the basis of phenetic considerations and outgroup comparison. A close correlation between morphology and chromosome cytology in the genus, then including some 110 species, led Goldblatt (1976b) to propose an infrageneric classification that used cytology as a major determinant in circumscribing subgenera and sections. Later research in *Moraea* and related genera led to the realization that *Moraea* as so circumscribed was paraphyletic when *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandris* Parl., *Hexaglottis* Vent., *Homeria* Vent. and *Roggeveldia* Goldblatt were recognized. A phylogenetic study of *Moraea* based on DNA sequence data subsequently confirmed this conclusion, thus fully supporting its expanded circumscription (Goldblatt *et al.* 2002). This study and a second, more extensive one (Schnitzler *et al.* 2011) also showed that Goldblatt's 1976 infrageneric classification of *Moraea* required considerable revision if a classification follow-

ing the principle of monophyly was to be implemented. In these molecular systematic studies some large species clusters comprised clades receiving moderate to strong support, but subg. *Moraea* included several disparate elements and required major restructuring to achieve a classification consistent with the phylogenetic principle of monophyly.

Some of the major changes include removal from subg. *Vieusseuxia* (D. Delaroché) Baker of sect. *Polyanthes* Goldblatt, which comprises a clade outside the subgenus and is sister to two lineages until now included in subg. *Moraea*. In addition, several individual species were shown by molecular, and sometimes cytological, data to be misplaced to subgenus or section. Re-evaluation of their morphology makes it clear that their position in the classification must be revised. This paper provides a new classification of *Moraea* based as far as possible on the principle of monophyly. *Moraea* now includes some 214 species, which we assign to 11 subgenera, 15 sections and three series. We also provide a full synopsis of the genus.

## MATERIALS AND METHODS

Chromosome data for *Moraea* were obtained from studies by Goldblatt (1976a, 1976b) and later papers (most importantly Goldblatt 1981, 1986b, 1986c) and some chromosome counts not yet published (Goldblatt & Manning 2013). Morphological information is from Goldblatt (1976a, 1976b, 1981, 1986a) and several later papers.

The molecular studies of Goldblatt *et al.* (2002) and Schnitzler *et al.* (2011) are summarized here and provide the framework for the revised classification. Some 161 species were included in the latter study, and three additional taxa have been sequenced for the present

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TABLE 1.—Additional *Moraea* species sequenced in this study with voucher information and GenBank/EMBL accession number for each gene region. Accession numbers for taxa not listed here can be found in Goldblatt *et al.* (2002) and Schnitzler *et al.* (2011).

Species	Voucher	rbcl	rps16	trnL-F
<i>Moraea intermedia</i> Goldblatt & J.C.Manning	Goldblatt, Manning & Porter 13405 (NBG)	JQ846027	JQ846024	JQ846030
<i>Moraea nubigena</i> Goldblatt	Helme s.n. (NBG)	JQ846028	JQ846025	JQ846031
<i>Moraea pearsonii</i> Goldblatt & J.C.Manning	Manning 3128 (NBG)	JQ846029	JQ846026	JQ846032

study, over 75% of the genus (Table 1). PCR amplification and sequencing were performed as described in Goldblatt *et al.* (2002). Insertions/deletions (indels) were coded as present/absent following the ‘simple indel coding’ method of Simmons & Ochoterena (2000), implemented in SeqState (Müller 2005). The final matrix comprised 3 096 characters from three plastid markers (*rbcl*, *rps16*, and *trnL-F*) and 218 indels. Maximum parsimony analyses were performed using the heuristic search implemented in PAUP\* (v. 4.0b10; Swofford 2002). Initial searches were carried out using 1 000 replicates of random taxon addition and the tree bisection and reconnection (TBR) algorithm with equal character weights, retaining a maximum of 10 trees per replicate. The resulting trees were used as starting trees in a second search using the same parameters with a limit of 10 000 trees, which were then used to reweight the characters according to the rescaled consistency index (RC). Successive searches were performed using the reweighted matrix until tree lengths reached stationarity. We performed 1 000 bootstrap replicates using equal character weights and the TBR swapping algorithm, again keeping only 10 trees at each step. Maximum likelihood analyses were performed in RAXML (v. 7.2.1; Stamatakis 2006) using the BINGAMMA function, with the alignment divided into partitions according to gene regions. This process implements the GTR+ $\Gamma$  model for each gene with individual estimation and optimization of model parameters and a discrete morphological model as proposed by Lewis (2001) for the indels, which is comparable to the Jukes-Cantor model of nucleotide substitution. We performed 500 rapid bootstrap searches (Stamatakis *et al.* 2008), followed by a thorough ML search on the original alignment. Bayesian phylogenetic inference was performed using MrBayes (v.3.2.1; Huelsenbeck & Ronquist 2001). The best-fit models of nucleotide evolution were implemented according to the Akaike Information Criterion (AIC) scores for substitution models evaluated using MrModeltest (v.2.3; Nylander 2004). For binary traits, MrBayes implements an F81-like model. Three independent runs with four chains each were run for 30 000 000 generations, sampling the Markov chain every 1 000 generations. After removal of the first 3 000 000 generations as burn-in, all runs were combined to build the consensus tree. The alignment and consensus trees are available from Tree-Base (accession number S13606).

DISCUSSION

All approaches resulted in highly congruent tree topologies. The phylogenetic tree presented here reflects the

topology and branch length of the Maximum Likelihood analysis. Unless indicated otherwise, support values reported in the text (e.g. 1, 95, 92) represent Bayesian posterior probabilities (if higher than 0.5), and bootstrap support values from the Maximum Likelihood and Maximum Parsimony analyses (if higher than 50%), respectively. Most of the major species clusters correspond to existing, named infrageneric taxa but their relationships to one another are often quite different from past interpretations of their affinities. Not entirely surprisingly, several species of uncertain affinity based on morphological considerations remain unresolved in the molecular analyses, notably *M. cooperi*, *M. nubigena* and *M. papilionacea*. The relationships of other species of which the affinities were uncertain, e.g. *M. fergusoniae* and *M. radians*, are established in the trees generated. Conversely, a few species appear in the molecular trees in positions unacceptable on morphological grounds, especially *M. inclinata* and *M. rivulicola*. These exceptions are discussed in more detail below in our proposed classification.

1. Subg. *Plumariae*: *Moraea lugubris* is linked with low significant statistical support (pp = 0.55, 67 BP(MP)) to the *M. bubalina* clade (Figure 1) in an association without morphological support. This taxonomically isolated species was retrieved as sister to all other species of *Moraea* in an earlier analysis (Goldblatt *et al.* 2002). *M. lugubris* is unique in *Moraea* in having coarsely netted corm tunics not matched elsewhere in *Moraea*, plumose style crests and stigmas located at the distal tips of the bifurcate style branches rather than as discrete lobes abaxial to the style branches. We recognize the monotypic subg. *Plumariae* for *M. lugubris*. Both the position of the stigmatic surfaces and the plumose style branches recall the genus *Ferraria*, which is well established as sister genus to *Moraea* (Goldblatt *et al.* 2002, 2008).

2. Subg. *Visciramosae*: the eight species of subg. *Visciramosae* (six included in the current phylogenetic analysis) are united by at least three morphological synapomorphies, notably sticky stems, unique brown,  $\pm$  woody, longitudinally grooved corm tunics with a sticky secretion on the inner surfaces, and stigmatic lobes with a central forked tooth. The  $\pm$  free but closely contiguous filaments of some species of the alliance are also unique in *Moraea*, but might constitute an ancestral state (other *Moraea* species have filaments partially or completely united except in some species of the very derived *M. tripetala* complex and in *M. thomasiae*, both subg. *Vieusseuxia*). *Ferraria*, sister genus to *Moraea*, has partially united filaments in all species. Floral mor-



phology is unremarkable in subg. *Visciramosae* except in the species with free filaments and in those with the style branches reduced and lacking crests and the inner tepals as well as the outer with nectar guides (a derived condition that recurs in several other clades). *M. simplex* stands out here in having filiform style branches extending between the stamens, a condition shared by the unrelated *M. fistulosa* and *M. monticola* (assigned here to sect. *Pseudospicatae* of subg. *Polyanthes*, although neither was included in the molecular analysis).

The members of subg. *Visciramosae* comprise two separate, well supported (both  $pp = 1$  and  $> 90$  BP) clades (Figure 1). One, including the multi-leaved *Moraea bubalina* and *M. vespertina*, is weakly linked with *M. lugubris* and the other, including the remaining species, which are characterized by presence of two foliage leaves, is placed as sister to the rest of the genus with only moderate support. The clear morphological synapomorphies that the two clades share (sticky stems, sigmoid branching, unique corm type, stigmatic appendages) provide adequate justification for ignoring the weak molecular data in treating both lineages within a single subg. *Visciramosa*. We recognize the two lineages as separate sections, *Multifoliae* and *Visciramosae*.

3. Subg. *Umbellatae*: *M. longiflora* (sect. *Tubiflora* Goldblatt), plus several species from sect. *Moraea* (*M. intermedia*, *M. margaretae*, *M. nana* and *M. umbellata*) were retrieved as a well-supported clade (1, 99, 96; Figure 1) sister to *M. maximiliani*. The second member of sect. *Tubiflora*, *M. cooperi*, was retrieved in an isolated but only weakly supported / unsupported (4–14 BP) position (Figure 1). We find it most unlikely that the molecular topology reflects the true relationships of *M. cooperi* as the morphological evidence linking it to the *M. intermedia* clade (i.e. subg. *Umbellatae*) is strong. Unique brown corm tunics, woody with plane surface (without the sticky secretion on the brown, longitudinally grooved corm tunics of subg. *Visciramosa*), darkly veined, pale yellow tepals, blunt outer inflorescence spathes usually not sheathing distally, and flowers with a perianth tube are all evidently derived character states that are shared with *M. longiflora* of the subgenus. Those features in *M. cooperi* may be homoplasious, but it seems to us unlikely that the entire set could have evolved independently. Thus we prefer to place *M. cooperi* in subg. *Umbellatae* rather than recognize it as a separate genus with the same morphological circumscription as subg. *Umbellatae*. We include eight species in what we designate subg. *Umbellatae* (one species, *M. linderi*, was not included in the molecular analysis). We note that *M. maximiliani* was retrieved as sister to the remaining members of the subg. *Umbellatae* clade and its position is weakly supported; nevertheless, it has the morphological synapomorphies of the subgenus hence its inclusion therein. We see no need for its recognition as a separate, monospecific subgenus or section in light of the morphology.

Floral diversification in the subgenus parallels that in subg. *Visciramosae*, ranging from an unspecialized *Moraea*-type flower with well developed style branches and crests and larger outer tepals bearing nectar guides, to reduced style branches lacking crests (*M. maximiliani*, *M. umbellata*) and, in *M. nana*, to style branches

represented by paired, filiform arms extending on either side of the opposed stamen. The flower type in *M. nana* is convergent with that in the *Hexaglottis* group (subg. *Polyanthes* sect. *Hexaglottis*), in *M. hexaglottis* (not sequenced) and in *M. pearsonii* (now subg. *Polyanthes* sect. *Pseudospicatae*).

4. Subg. *Moraea*: here much reduced in size, includes *M. vegeta*, type of the genus, plus *M. gawleri* and its close relative, *M. vlokii*, which together form a well-supported clade (1, 100, 99). The phylogenetic position of this clade (sister to the first polytomy in the tree) was, however, not supported in the bootstrap analyses and thus remains uncertain. To this small alliance we provisionally add *M. namaquamountana* and *M. indecora*, a rare Namaqualand endemic, and not yet sequenced.

*Moraea garipensis* and *M. ramosissima* constitute another small clade (1, 100, 100) included by Goldblatt (1976b, 1986a) in subg. *Moraea*. A separate subgenus for the two species seems unwarranted as the molecular topology here is not well supported and we therefore provisionally retain them as a section of subg. *Moraea* pending additional molecular studies. At the morphological level, the species of subg. *Moraea* share pale-coloured corm tunics, mostly of fine fibres, except for *M. garipensis* and *M. ramosissima*. Further molecular analysis may show an alternative placement for these two species, the brown corm tunics of which recall those of subg. *Umbellatae*.

The rare Western Cape mountain endemic *Moraea nubigena* appears as isolated in the molecular phylogeny (Figure 1) as it does morphologically. The acaulescent habit, solitary leaf and unbranched stem are all distinctive but may be adaptations to its montane habit. Goldblatt (1986a) linked the species to *M. lugubris*, but that now seems unlikely. *M. nubigena* has a chromosome number of  $n = 10$  and a fugaceous flower, both plesiomorphic in *Moraea*, and finely fibrous corm tunics, evidently an apomorphy for subg. *Moraea* but the blue perianth is otherwise unknown in the subgenus. We provisionally include it in subg. *Moraea*, with which the corm tunics are consistent, but it is not referred to any section. We note that it is the only blue-flowered and single-leaved member of the group. An argument can be made for the alternative, a separate subgenus for *M. nubigena*, but we see no value in a monospecific subgenus for the species.

5. Subg. *Monocephalae*: the lineage including *Moraea angusta* and two immediately related species is moderately well-supported (1, 89, 65) as one of a polytomy (Figure 1). The alliance (including *M. valisavium*, not sequenced) is united by unbranched stems, a single foliage leaf inserted well above ground level, a terete leaf blade, obtuse to truncate inflorescence spathes, sticky nodes, a prismatic ovary, and flattened, discoid seeds. The alliance was treated as the rank-less group *Monocephalae* by Baker (1896, then including *M. spathulata* of subg. *Grandiflora*), and as subg. *Monocephalae* by Goldblatt (1976b). Although *M. namaquamountana* is retrieved as sister to the *M. angusta* clade in all molecular analyses, this association is without statistical or morphological support and there is little reason to doubt that *M. namaquamountana* is allied to

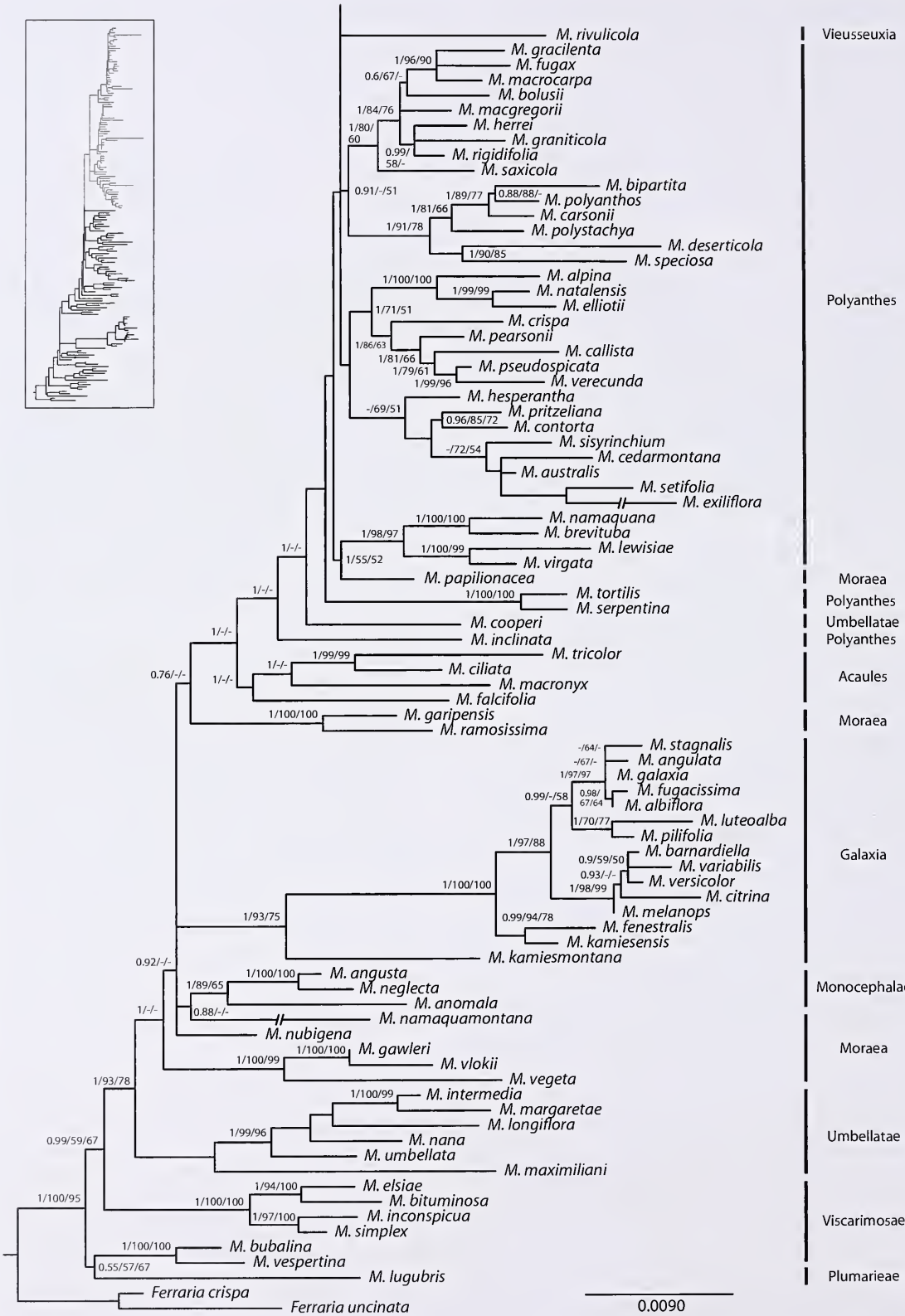
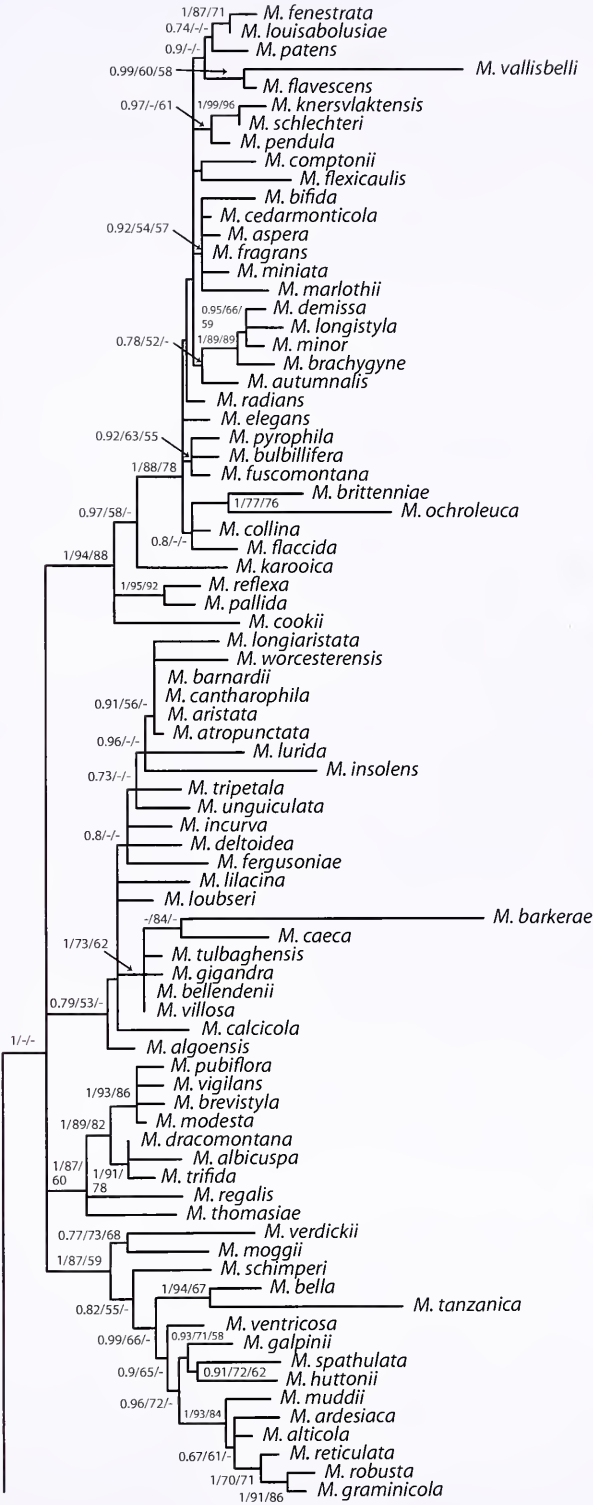
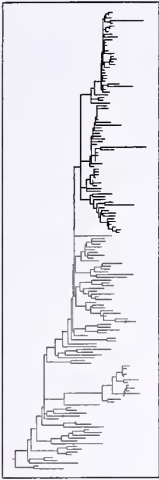


FIGURE 1.—Maximum Likelihood phylogeny of *Moraea*. Support values at nodes are Bayesian posterior probabilities, and bootstrap values from the Maximum Likelihood and Maximum Parsimony analyses respectively if pp > 0.5, or BS > 50%. The subgeneric classification is indicated by black bars on the right.



Homeria

Vieusseuxia

Grandiflorae



*M. gawleri* (subg. *Moraea*), with which it shares a virtually identical flower, a distinctive, asymmetric corm, and globose capsules. The *M. angusta* alliance is phylogenetically isolated and well defined by several morphological synapomorphies, and we continue to accord it subgeneric rank.

6. Subg. *Galaxia*: all species previously treated as the genus *Galaxia* (Goldblatt 1984a) comprise a well-supported (1, 93, 75) clade. The alliance has several synapomorphies, not least an acaulescent habit, flowers always with a perianth tube, style branches short and lacking crests, and an asymmetric corm, and we recognize it as subg. *Galaxia*. Relationships within subg. *Galaxia* are more complex than reflected in Goldblatt's (1979b) recognition of two sections. Although sect. *Eurystigma* (species with entire style branches) is retrieved as monophyletic, sect. *Galaxia* (species with fringed style branches) is shown to comprise two lineages, the *M. galaxia* clade and *M. kamiesensis* plus *M. fenestralis*. A strictly phylogenetic classification would thus require the recognition of three or four sections, but we do not feel that this is justified in such a small group and suggest that the level of series is adequate. The position of the isolated *M. kamiesmontana* in the tree (Figure 1) as sister to the remaining members of the clade has morphological support; it is the only member of the subgenus that has clawed tepals, the plesiomorphic condition in *Moraea*. We thus admit three series, *Eurystigma*, *Galaxia* and *Unguiculatae*, this last monospecific.

7. Subg. *Acaules*: the species of the taxonomically isolated *Moraea ciliata* group were retrieved with strong support in the Bayesian analysis (pp = 1) as sister to the remaining species of *Moraea* and we accord the group subgeneric status. Within the group *M. ciliata*, *M. macronyx* and *M. tricolor* are obviously closely related, with the morphologically somewhat different *M. falcifolia* as sister. One more species belongs here, *M. longipes*, until recently included in *M. ciliata* (Goldblatt & Manning 2009). Synapomorphies for subg. *Acaules* include leaves clustered at the terminal node, stem usually below ground level at flowering time (not *M. longipes*), sessile flowers raised above the leaves and inflorescence spathes on an elongating, tubular stalk; possibly the sterile base of the ovary (called a contractile pedicel in older literature) that retracts after flowering. The alliance was treated as sect. *Acaules* by Goldblatt (1976b), following Baker (1896).

8. Subg. *Polyanthes*: the *Moraea serpentina*-*M. tortilis* species pair (1, 100, 100) is weakly placed as sister to the remaining species in the genus, but without statistical support. On morphological grounds, we include the six main clades (Figure 1) of this large group, including *M. serpentina*-*M. tortilis*, as sections of subg. *Polyanthes*. The alliance is united morphologically by distinctive blackish, wiry corm tunic fibres, but the multi-leaved habit (reduced in some species to a single leaf) and fugaceous flower are plesiomorphic. We note that, in addition, many species of the subgenus have an apomorphic, included ovary, but the condition is reversed in two sections. The subgenus is mixed for chromosome number: a base number of  $x = 20$  is ancestral and basic for two sections, *Serpentinae* and *Deserticola* (but reduction to  $x = 6$  (or 5) has occurred within

sect. *Deserticola*) and  $x = 6$  is almost exclusive in sect. *Hexaglottis*, sect. *Gynandris*, sect. *Polyanthes* and sect. *Pseudospicatae* (one species of sect. *Polyanthes*, *M. inclinata* has  $n = 6$  and 11).

In the molecular analyses, *Moraea rivulicola* is retrieved in an unresolved polytomy in subg. *Polyanthes*, but without any statistical support. This species has all the morphological hallmarks of subg. *Viessieuxia* as we noted in an earlier molecular analysis (Goldblatt *et al.* 2002) and sequences of a second and third sample of the species alters this topology hardly at all, ruling out experimental error. Another species that appears misplaced here on morphological grounds is *M. exiliflora*, which almost certainly belongs in sect. *Polyanthes* according to morphology. We have no explanation for the apparently anomalous position of these two species in our trees, but to suggest that their morphology is somehow convergent with those clades to which morphology suggest they belong, is unacceptable. The remaining species of the clade, which comprise sect. *Gynandris* (Goldblatt 1998), and originally the genus *Gynandris* (Goldblatt 1980b), have apomorphic, translucent inflorescence spathes and a sessile ovary with a tubular, sterile beak, which leaves no doubt that it is a monophyletic alliance. The clade receives moderate support in the molecular analyses (69 and 51 BP, respectively; pp = 0.6, but excluding *M. exiliflora*). Two species of sect. *Gynandris*, *M. sisyrinchium* and *M. mediterranea* (= *G. monophylla* Boiss. & Heldr. ex Klatt and not sequenced), occur in the Mediterranean Basin and Middle East and constitute the only species of *Moraea* that occur north of the Sahara.

Sect. *Hexaglottis* [the genus *Hexaglottis sensu* Lewis (1959) and Goldblatt (1987)] has the derived, *Hexaglottis*-type flower with subequal, spreading tepals with short claws and style branches reduced to filiform arms extended on either side of the opposed stamen. The inclusion of *M. papilionacea* in the clade (Figure 1) receives only weak support in the bootstrap analyses (55 and 42 BP, respectively) and has no morphological basis, but the affinities of this species are uncertain and we prefer to retain it as unplaced in subg. *Moraea*, to which it was assigned by Goldblatt (1976b, 1986a).

Sect. *Pseudospicatae* (1, 71, 51), sect. *Deserticola* (1, 80, 60) and sect. *Polyanthes* (1, 91, 78) are retrieved as monophyletic in the molecular analysis and are also morphologically coherent. The members of sect. *Polyanthes sensu* Goldblatt (1976b, 1986a) fall in two lineages; the first (here sect. *Polyanthes*) mostly with multiple leaves and the second (sect. *Pseudospicatae*) with a single leaf. Both clades include species with typical *Moraea*-type flowers as well as others with reduced style branches and style crests. We include *M. inclinata* in sect. *Pseudospicatae* without hesitation, despite its anomalous position in the tree, sister to *M. cooperi* plus the rest of the genus. It has a single leaf, blue flower, exerted ovary and capsule, and basic chromosome number of  $x = 6$ , all of which accord with this decision. It is allied to, and sometimes has been included in, *M. natalensis* of sect. *Pseudospicatae*. Although sect. *Deserticola* (unranked *Subracemosae* Baker) likewise has species with the typical *Moraea* flower and others with reduced style branches and crests (the *M. rigidi-*

*folia-M. herrei* clade, BP 54), all members consistently have the ovary included in the spathes. The ovary is sessile in *M. herrei* and has a sterile beak, also present in a less developed state in *M. rigidifolia* and the *M. fugax* group (1, 96, 90). Sect. *Deserticola* closely resembles sect. *Serpentinae* in several morphological features and we would not be surprised if additional molecular data show them to be a clade. The available molecular data, however, preclude their union.

Subg. *Polyanthes* is sister to a polytomy formed by four large clades that include the remaining species in the genus. Two of these coincide exactly with subg. *Grandiflora* sensu Goldblatt (1976b) and subg. *Homeria* sensu Goldblatt (1981); and we continue to treat them as subgenera rather than sections because of their large size.

9. Subg. *Grandiflorae*: this subgenus (1, 87, 59) includes some 28 species of eastern, southern and tropical Africa. Most are tall, have unbranched stems and large, evidently unspecialized flowers that are long-lived in almost all species. All have a solitary leaf, distinctive, flattened, discoid seeds and a karyotype of large, subacrocentric chromosomes with a base number of  $x = 6$ . With only half its species sequenced for the molecular study, subg. *Grandiflora* is still inadequately sampled and no clear morphological patterns are evident in the tree topology.

10. Subg. *Vieusseuxia*: we treat the remaining two clades as constituting subg. *Vieusseuxia*, which has until now included sect. *Vieusseuxia* of Goldblatt (1976b) plus the monospecific sect. *Integres*. All species share a basic chromosome number of  $x = 6$ , but often a somewhat variable karyotype, although always of relatively large chromosomes. Members of the subgenus have derived, long-lived flowers (a fugaceous flower is plesiomorphic in *Moraea*), a single foliage leaf, also derived (multiple leaves only in *M. fergusoniae* must be interpreted as a striking reversal), and inner tepals that are typically much reduced, often 3-lobed or even absent.

There is no morphological support for the two separate clades (1, 87, 60 and 0.79, 53, respectively; Figure 1), and there are few obvious subclades in subg. *Vieusseuxia* that correlate with morphological patterns. A separate analysis of the alliance including additional molecular markers is probably needed to better resolve the phylogeny.

*Moraea fergusoniae* (included in subg. *Moraea* by Goldblatt 1976b) is inconsistent in subg. *Vieusseuxia* in its several leaves, but is shown to be nested in the subgenus, where its basic chromosome number,  $x = 6$ , and trilobed inner tepals accord perfectly. We include it here without hesitation. The Cape species, *M. thomasiae*, separated by Goldblatt (1986a) as sect. *Integres* on account of its entire inner tepals, yellow flowers (rare in the subgenus) and  $\pm$  free stamens, is morphologically isolated in subg. *Vieusseuxia* and we continue to refer it to a separate section. In the tree (Figure 1) it is allied with a second winter-rainfall species, *M. regalis* (possibly misplaced here and without morphological support), plus all the eastern southern African (and summer rainfall area) species of subg. *Vieusseuxia*, which constitute a well

supported (1, 87, 60) lineage. It is biogeographically significant that these eastern species constitute a clade, thus representing a minor radiation of the genus in the region.

We segregate the remaining species of subg. *Vieusseuxia* (BP 98) in two sections based primarily on morphology. These are the small sect. *Villosae*, which includes the species clustered around *M. villosa* and which share outer tepal limbs as wide or wider than long and usually both leaves and stems pilose (not *M. caeca*). The remaining species fall by default in sect. *Vieusseuxia*: molecular analysis provides modest support for this alliance (1, 73, 62; excluding *M. calcicola*). The isolated position of *M. algoensis* (sister to sect. *Vieusseuxia* plus sect. *Villosae*) and the position of *M. barkerae* in the *M. villosa* clade receive no morphological support and both are provisionally referred to sect. *Vieusseuxia*.

11. Subg. *Homeria*: this exclusively southern African alliance is well supported (1, 94, 88) in the molecular analysis and is united morphologically by its hard, black corn tunic fibres and by specialized flowers in which the style branches and crests are reduced, the crests sometimes lacking, and the inner tepals are scarcely smaller than the outer (the *Homeria*-type flower sensu Goldblatt (1986c)). Both fugaceous and long-lived flowers are present in the subgenus. Basic chromosome number is  $x = 6$ , but a few species have  $n = 5$  or 4 (and  $2n = 9$ ). Leaf number is reduced in some species from several to consistently one leaf, evidently the derived condition. The inclusion of *M. radians* in the subg. *Homeria* clade (originally a separate genus *Sessilistigma*) is consistent with Goldblatt's (1991) reduction of the genus in *Homeria*. *M. flexicaulis*, originally assigned to a monotypic section of *Moraea* (Goldblatt 1982) is likewise retrieved within the subg. *Homeria* clade, which is consistent with its chromosome number and karyotype. We have no hesitation in including it in subg. *Homeria*. Its rather unusual morphology (the stem is strongly flexuose and the flowers have well developed style branches and crests) is somewhat anomalous for the subgenus, but recall the species pair *M. knersvlaktensis* and *M. schlechteri* (originally treated as *Homeria* sect. *Namaquanae* by Goldblatt (1981)) and we provisionally unite the three species in an enlarged sect. *Flexuosae* (the earliest name in *Moraea* for the section). There is no molecular support for the inclusion of *M. louisabolusiae* with these species as proposed by Goldblatt (1981, as *H. bolusiae*) based on morphology. We place *M. louisabolusiae* in sect. *Homeria* close to *M. patens*; a treatment consistent with both morphology and the molecular tree topology. Within the subgenus, the group of species around *M. cookii* also merits taxonomic recognition and we treat the alliance as sect. *Stipantherae* Goldblatt (1981). It then comprised five species with the single leaf clasping the stem for some distance, fugaceous flowers and, in four species, the filaments free distally. Of the five species *M. britteniae* and *M. marlothii* fall outside the clade and their continued inclusion in sect. *Stipantherae* must be viewed as provisional.

There is no molecular support for species groups based on flower shape, namely those with very short tepal claws clasping the base of the filament column (e.g. sect. *Conantherae* including *Moraea bifida*, *M. miniata*, *M. pendula* and several more) versus those



with longer claws forming a wide, deep bowl (e.g. sect. *Homeria*, including *M. collina*, *M. minor*, *M. ochroleuca*, *M. pyrophila* and others). In fact, apart from three members of sect. *Stipantherae* and two of sect. *Flexuosae*, there are no significant species alliances retrieved in the molecular trees that merit taxonomic recognition and we fall back on the existing classification based on morphology in which two more sections were recognized (Goldblatt 1981): sects. *Conantherae* and *Homeria* as well as sect. *Flexuosae* and sect. *Stipantherae*. Separate molecular study of subg. *Homeria* using additional DNA sequences may help resolve relationships and provide a test for the current classification.

#### CLASSIFICATION AND SYNOPSIS OF *MORAEA*

***Moraea* Mill.**, Figures of Plants vol. 2: 159, t. 238 (1758) (as *Morea*), name and spelling conserved. Type also conserved: *M. vegeta* L.

1. Subg. **Plumariae** Goldblatt & J.C.Manning, subg. nov. Type species: *M. lugubris* (Salisb.) Goldblatt.

Plants with branched stems. *Foliage leaves* several, channelled. *Flowers* fugaceous, blue; tepals subequal but outer larger and with nectar guides, limbs laxly spreading; filaments united in lower half; style branches diverging at tips and stigmatic apically, crests plumose. *Capsules* ± globose. *Basic chromosome number*  $x = 10$ .

1. *M. lugubris* (Salisb.) Goldblatt

2. Subg. **Visciramosae** Goldblatt in Annals of the Missouri Botanical Garden 63: 7 (1976b). Type species: *M. bituminosa* (L.f.) Ker Gawl.

Plants with branched stems, nodes sticky; corm tunics ± woody, sticky on adaxial surface. *Foliage leaves* several or 2, channelled. *Flowers* fugaceous, variously coloured; tepals subequal or outer larger and with nectar guides, limbs reflexed; filaments united in lower half or free but contiguous; style branches broad with abaxial stigmatic lobe bearing a forked appendage in centre and well developed paired crests or style branches reduced, lacking crests, then flattened or filiform. *Capsules* ± globose. *Basic chromosome number*  $x = 10$ .

2a. Sect. **Multifoliae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. vespertina* Goldblatt & J.C.Manning.

*Foliage leaves* several. *Flowers* white, pale blue or predominantly buff-brown; style branches and crests moderately or well developed.

2. *M. vespertina* Goldblatt & J.C.Manning

3. *M. bubalina* Goldblatt

2b. Sect. **Visciramosae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. bituminosa* (L.f.) Ker Gawl.

*Foliage leaves* 2. *Flowers* yellow, blue or brown, occasionally white; style branches and crests moderately well developed or reduced and without crests (in *M. simplex* filiform and extending between the stamens).

4. *M. bituminosa* (L.f.) Ker Gawl.

5. *M. inconspicua* Goldblatt

6. *M. viscaria* (L.f.) Ker Gawl.

7. *M. saldanhae* Goldblatt & J.C.Manning

8. *M. elsiae* Goldblatt

9. *M. simplex* Goldblatt & J.C.Manning

3. Subg. **Umbellatae** Goldblatt & J.C.Manning, subg. nov. Type: *M. margaretae* Goldblatt.

*Rheome* Goldblatt: 92 (1980a). Type species: *R. maximiliani* (Schltr.) Goldblatt (= *Moraea maximiliani* (Schltr.) Goldblatt).

Plants with branched stems, branches and leaves usually clustered at first aerial node; corm tunics dark brown, initially unbroken, later splitting irregularly. *Foliage leaves* several or solitary. *Inflorescence spathes* blunt or truncate, with outer spathe often diverging apically. *Flowers* fugaceous, pale yellow to ± beige (rarely pale pink) with dark venation, sometimes with perianth tube; stamens united in lower half; style branches well developed or reduced and lacking crests (in *M. nana* with paired filiform arms extended horizontally). *Capsules* ± club-shaped. *Basic chromosome number*  $x = 10$ .

10. *M. linderi* Goldblatt

11. *M. margaretae* Goldblatt

12. *M. intermedia* Goldblatt & J.C.Manning

13. *M. cooperi* Baker

14. *M. longiflora* Ker Gawl.

15. *M. umbellata* Thunb.

16. *M. maximiliani* (Schltr.) Goldblatt

17. *M. nana* (L.Bolus) Goldblatt

4. Subg. **Moraea**

*Moraea* rankless *Corymbosae* Baker: 10 (1896), nom. illegit. superfl. Type species: *M. juncea* L. = *M. vegeta* L., type of the genus.

Plants with stems usually branched, sometimes repeatedly; corm tunics finely to coarsely fibrous or ± woody. *Foliage leaves* several to 2(1). *Flowers* mostly yellow to buff-brown, occasionally pink to red, or partly white (blue in *M. nubigena*); filaments united in lower half; style branches and crests well developed (reduced in *M. vlokii*). *Capsules* ± globose, exserted. *Basic chromosome number*  $x = 10$ .

4a. Sect. **Moraea**

*Corms* often asymmetric; tunics of pale, coarse or fine fibres. *Foliage leaves* several to 2(1). *Flowers* yellow, sometimes pink to red or brown; filaments partially united; style branches and crests usually well developed (not *M. vlokii*).

18. *M. vegeta* L.

19. *M. indecora* Goldblatt

20. *M. gawleri* Spreng.

21. *M. vlokii* Goldblatt

22. *M. namaquamontana* Goldblatt

4b. Sect. **Polyphyllae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. ramosissima* (L.f.) Ker Gawl.

Plants usually multi-branched. *Corm* tunics brown,



fragmenting irregularly. *Foliage leaves* several to many, broad and prominently channelled. *Flowers* yellow; filaments united in lower half or only at base; style branches and crests well developed.

23. *M. ramosissima* (L.f.) Druce

24. *M. gariopensis* Goldblatt

Uncertain position and provisionally placed here:

25. *M. papilionacea* (L.f.) Ker Gawl.

26. *M. nubigena* Goldblatt

5. Subg. **Galaxia** (Thunb.) Goldblatt & J.C.Manning, stat. nov. *Galaxia* Thunb.: 50 (1782). *Moraea* sect. *Galaxia* (Thunb.) Goldblatt: 376 (1998). Type species: *G. graminea* Thunb., lecto. designated by Phillips (1951) = *Moraea fugacissima* (L.f.) Goldblatt.

Plants acaulescent at anthesis; corm tunics pale, usually finely fibrous. *Leaves* several, often plane and  $\pm$  prostrate, narrowly channelled or terete, hardly distinct from spathes. *Flowers* fugaceous, sessile, with solid perianth tube, yellow, white, or shades of pink to purple; tepals mostly without narrow claws (not *M. kamiesmontana*); style branches much reduced with crests obscure, stigma lobes entire or irregularly fringed. *Capsules*  $\pm$  globose. *Basic chromosome number*  $x = 9$ .

5a. Series **Unguiculatae** Goldblatt & J.C.Manning, ser. nov. Type species: *M. kamiesmontana* (Goldblatt) Goldblatt.

*Flowers* pink with white cup; tepals prominently clawed; filaments partly united; style branches with stigma lobes entire.

27. *M. kamiesmontana* (Goldblatt) Goldblatt

5b. Series **Eurystigma** (Goldblatt) Goldblatt in Novon 8: 377 (1998). *Galaxia* subg. *Eurystigma* Goldblatt: 398 (1979a,b). *Galaxia* ser. *Eurystigma* (Goldblatt) Goldblatt: 376 (1998). Type species: *G. versicolor* Salisb. ex Klatt (= *Moraea versicolor* (Salisb. ex Klatt) Goldblatt).

*Flowers* pink to purple or white (yellow in *M. citrina*); filaments largely united; style branches with stigma lobes entire.

28. *M. citrina* (G.J.Lewis) Goldblatt

29. *M. barnardiella* Goldblatt

30. *M. melanops* Goldblatt & J.C. Manning

31. *M. versicolor* (Salisb. ex Klatt) Goldblatt

32. *M. variabilis* (G.J.Lewis) Goldblatt

33. *M. minima* Goldblatt

34. *M. fenestralis* (Goldblatt & E.G.H.Oliver) Goldblatt

5c. Series **Galaxia** (Thunb.) Goldblatt in Novon 8: 376 (1998). *Galaxia* Thunb.: 50 (1782). Type species: as for subgenus.

*Flower* yellow or white, filaments largely united or spreading from base (*M. luteoalba*); style branches with fringed stigma lobes.

35. *M. kamisensis* Goldblatt

36. *M. luteoalba* (Goldblatt) Goldblatt

37. *M. galaxia* (L.f.) Goldblatt & J.C.Manning

38. *M. pilifolia* Goldblatt

39. *M. vivuzela* J.C.Manning & Goldblatt

40. *M. albiflora* (G.J.Lewis) Goldblatt

41. *M. fugacissima* (L.f.) Goldblatt

42. *M. stagnalis* (Goldblatt) Goldblatt

43. *M. angulata* Goldblatt

6. Subg. **Monocephalae** (Baker) Goldblatt in Annals of the Missouri Botanical Garden 63: 7 (1976b). Rankless *Monocephalae* Baker: 10 (1896). Type species: *M. angusta* (Thunb.) Ker Gawl., lecto. designated by Goldblatt: 7 (1976b).

Plants unbranched, usually with sticky nodes. *Foliage leaf* solitary, distally terete. *Flowers* fugaceous, yellow to buff-brown; stamens united only near base; style branches well developed; ovary sharply 3-angular. *Capsules* ovoid-oblong. *Seeds* flattened and discoid. *Basic chromosome number*  $x = 10$ .

44. *M. angusta* (Thunb.) Ker Gawl.

45. *M. anomala* G.J.Lewis

46. *M. neglecta* G.J.Lewis

47. *M. vallisavium* Goldblatt

7. Subg. **Acaules** (Baker) Goldblatt & J.C.Manning, stat. nov. Rankless *Acaules* Baker: 8 (1896) [as 'sect. *Acaules* Baker' (Goldblatt 1976b)]. Type species: *M. ciliata* (L.f.) Ker Gawl.

Plants usually acaulescent (not *M. longipes*), usually unbranched, often with single rhpidium; corm tunics usually pale and coarsely fibrous. *Foliage leaves* several to few, hardly distinct from spathes, channelled. *Flowers* fugaceous, retracted after anthesis to base of rhpidium, various colours; stamens united in lower half; style branches well developed. *Capsules* concealed in spathes. *Basic chromosome number*  $x = 10$ .

48. *M. falcifolia* Klatt

49. *M. ciliata* (L.f.) Ker Gawl.

50. *M. longipes* Goldblatt & J.C.Manning

51. *M. tricolor* Andrews

52. *M. macronyx* G.J.Lewis

8. Subg. **Polyanthes** (Goldblatt) Goldblatt & J.C.Manning, comb. nov. *Moraea* sect. *Polyanthes* Goldblatt (1976b). Type species: *M. polystachya* (L.f.) Ker Gawl.

Corm tunics mostly of hard, black fibres. *Foliage leaves* several to solitary. *Flowers* fugaceous, mostly blue to mauve, also yellow or white; stamens united in lower half; ovary often included, style branches well developed with prominent crest or much reduced, sometimes as paired or single filiform arms. *Capsules* oblong-ellipsoid, sometimes beaked, exerted or included. *Basic chromosome number*  $x = 10$  but four sections have  $x = 6$ .

8a. Sect. **Serpentinae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. serpentina* Baker.

*Foliage leaves* 2 or 3, twisted or coiled. *Flowers* blue, yellow or mostly white; style branches and crests well developed. *Ovary* and *capsules* included.

53. *M. serpentina* Baker

54. *M. tortilis* Goldblatt

8b. Sect. **Deserticola** Goldblatt in Annals of the Missouri Botanical Garden 63: 7 (1976b). Type species: *M. bolusii* Baker.

Rankless *Subracemosae* Baker: 9 (1896) [as 'sect. *Subracemosae* Baker' in Goldblatt: 7 (1976b)]. Type species: *M. edulis* (L.f.) Ker Gawl. (= *M. fugax* (D.Delaroche) Ker Gawl.), lecto., designated by Goldblatt: 7 (1976b).

*Barnardiella* Goldblatt: 312 (1977a). Type species: *B. spiralis* (N.E.Br.) Goldblatt (= *Moraea herrei* (L.Bolus) Goldblatt).

Plants unbranched or branched, branches sometimes sessile. *Foliage leaves* solitary (sometimes 2 in *M. fugax* group). *Flowers* usually blue to mauve or violet (sometimes yellow or white); tepal claws short or ± as long as limbs; stamens united in lower half; style branches well developed with erect crests or reduced, without crests (as paired or filiform arms extended horizontally in *M. hexaglottis*). *Ovary* and *capsules* included, sometimes beaked.

55. *M. saxicola* Goldblatt

56. *M. macgregorii* Goldblatt

57. *M. namibensis* Goldblatt

58. *M. bolusii* Baker

59. *M. graniticola* Goldblatt

60. *M. herrei* (L.Bolus) Goldblatt

61. *M. rigidifolia* Goldblatt

62. *M. hexaglottis* Goldblatt

63. *M. fugax* (D.Delaroche) Ker Gawl.

64. *M. gracilentia* Goldblatt

65. *M. filicaulis* Baker

66. *M. macrocarpa* Goldblatt

8c. Sect. **Hexaglottis** (Vent.) Goldblatt in Novon 8: 376 (1998). *Hexaglottis* Vent.: 6 (1808). Type species: *H. longifolia* (Jacq.) G.J.Lewis, lecto. designated by Lewis: 219 (1959) = *M. longifolia* (Jacq.) Pers.

*Plantia* Herbert: 89 (1844). Type species: *P. flava* Herb. (probably = *Moraea virgata* Jacq.).

Plants usually branched, secondary branches usually sessile. *Flowers* yellow, with tepals subequal with claws short; tepals united in tube in 2 species; style branches reduced to paired filiform arms extended either side of opposed stamen, ovary exserted or included and ± sessile in species with perianth tube. *Ovary* and *capsules* exserted or included.

67. *M. namaquana* (Goldblatt) Goldblatt

68. *M. lewisiae* (Goldblatt) Goldblatt

69. *M. longifolia* (Jacq.) Pers.

70. *M. riparia* (Goldblatt) Goldblatt

71. *M. brevitiba* (Goldblatt) Goldblatt

72. *M. virgata* Jacq.

8d. Sect. **Gynandriris** (Parl.) Goldblatt in Novon 8: 376 (1998). *Gynandriris* Parl.: 49 (1854). *Iris* subg. *Gynandriris* (Parl.) Baker: 2 (1892). *Iris* sect. *Gynandriris* (Parl.) Dykes: 229 (1913). *Moraea* sect. *Gynandriris*

(Parl.) Goldblatt: 376 (1998). Type species: *M. sisyrinchium* (L.) Ker Gawl.

*Helixyra* Salisb. ex N.E.Br.: 348 (1929) [*Helixyra* Salisb., Trans. Hort. Soc. 1: 305 (1812), nom. nud.], nom. illeg. superfl. pro *Gynandriris*. Type species: not indicated by author.

*Moraea* subg. *Helixyra* Salisb. ex Baker [as a combination but *Helixyra* Salisb. nom. inval.]: 48 (1892). Type species: *M. simulans* Baker, lecto., here designated.

Plants unbranched or few-branched; spathes translucent with dark veins. *Flowers* fugaceous, blue to purple or white; stamens united in lower half; style branches well developed with erect crests; ovary ± sessile and with sterile tubular beak. *Capsules* with transparent walls, remaining enclosed in spathes.

73. *M. australis* Goldblatt

74. *M. setifolia* (L.f.) Druce

75. *M. cedarmontana* (Goldblatt) Goldblatt

76. *M. simulans* Baker

77. *M. sisyrinchium* (L.) Ker Gawl.

78. *M. mediterranea* Goldblatt

79. *M. pritzeliana* Diels

80. *M. contorta* Goldblatt

81. *M. hesperantha* (Goldblatt) Goldblatt

8e. Sect. **Polyanthes** Goldblatt in Annals of the Missouri Botanical Garden 63: 8 (1976b). Type species: as for subgenus.

Plants few- to several-branched. *Foliage leaves* several to 2. *Flowers* shades of blue to violet or purple (rarely yellow); style branches well developed with prominent crests or reduced and crests vestigial. *Ovary* and *capsules* usually exserted.

82. *M. bipartita* L.Bolus

83. *M. polystachya* (L.f.) Ker Gawl.

84. *M. venenata* Dinter

85. *M. speciosa* (L.Bolus) Goldblatt

86. *M. polyanthos* Thunb.

87. *M. deserticola* Goldblatt

88. *M. tanquana* Goldblatt & J.C.Manning

89. *M. carsonii* Baker

8f. Sect. **Pseudospicatae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. pseudospicata* Goldblatt.

*Roggeveldia* Goldblatt: 840 (1979c publ. 1980). Type species: *R. fistulosa* Goldblatt (= *Moraea fistulosa* (Goldblatt) Goldblatt).

Plants unbranched or branched, secondary branches sometimes sessile. *Foliage leaves* solitary (2 in *M. callista*, which may be misplaced here). *Flowers* usually blue to mauve or violet; tepal claws short or ± as long as limbs; stamens united in lower half; style branches well developed with erect crests or reduced, without crests, sometimes as paired or single filiform arms extended horizontally. *Ovary* and *capsules* exserted or included.

90. *M. elliotii* Baker

91. *M. exiliflora* Goldblatt

92. *M. alpina* Goldblatt

93. *M. stricta* Baker
94. *M. thomsonii* Baker
95. *M. natalensis* Baker
96. *M. inclinata* Goldblatt
97. *M. iringensis* Goldblatt
98. *M. afro-orientale* Goldblatt
99. *M. callista* Goldblatt
100. *M. crispa* Thunb.
101. *M. verecunda* Goldblatt
102. *M. pseudospicata* Goldblatt
103. *M. pearsonii* Goldblatt & J.C.Manning
104. *M. monticola* Goldblatt
105. *M. marginata* J.C.Manning & Goldblatt
106. *M. fistulosa* (Goldblatt) Goldblatt

9. Subg. **Grandiflorae** Goldblatt in Annals of the Missouri Botanical Garden 63: 8 (1976b). Type species: *M. spathulata* (L.f.) Klatt.

*Hymenostigma* Hochst. in Flora 27: 24 (1844). Type species: *H. schimperii* Hochst. (= *Moraea schimperii* (Hochst.) Pic.-Serm.).

*Iridopsis* Welw. ex Baker in Transactions of the Linnean Society of London, Botany 1: 270 (1878), pro syn.

Plants unbranched. *Flowers* yellow (white) or blue to violet; stamens united in lower half; ovary usually 3-angled; style branches well developed with prominent crests. *Capsules* large, exserted. *Seeds* flattened, discoid. *Basic chromosome number*  $x = 6$ .

107. *M. spathulata* (L.f.) Klatt
108. *M. moggii* N.E.Br.
109. *M. huttonii* (Baker) Oberm.
110. *M. alticola* Goldblatt
111. *M. reticulata* Goldblatt
112. *M. robusta* (Goldblatt) Goldblatt
113. *M. galpinii* (Baker) N.E.Br.
114. *M. muddii* N.E.Br.
115. *M. ardesiaca* Goldblatt
116. *M. carnea* Goldblatt
117. *M. graminicola* Oberm.
118. *M. hiemalis* Goldblatt
119. *M. unibracteata* Goldblatt
120. *M. bella* Harms
121. *M. macrantha* Baker
122. *M. textilis* Baker
123. *M. ventricosa* Baker
124. *M. schimperii* (Hochst.) Pic. Serm.
125. *M. verdickii* De Wild.
126. *M. tanzanica* Goldblatt
127. *M. brevifolia* Goldblatt
128. *M. inyangani* Goldblatt
129. *M. angolensis* Goldblatt
130. *M. upembana* Goldblatt
131. *M. clavata* Goldblatt
132. *M. bovonei* R.C.Foster
133. *M. balundana* Chiov.
134. *M. unifoliata* Goldblatt

10. Subg. **Viusseuxia** (D.Delaroche) Baker, Handbook of the Irideae: 48 (1892). *Viusseuxia* D.Delaroche: 31 (1766). Type species: *V. spiralis* D.Delaroche, lectotype designated by Goldblatt: 8 (1976b) = *M. bellendenii* (Sweet) N.E.Br.

*Phaianthes* Raf.: 30 (1836). Type species: *P. lurida* (Ker Gawl.) Raf. (= *Moraea lurida* Ker Gawl.).

Plants simple or few-branched; corm tunics of brown firm to soft fibres. *Foliage leaf* solitary (several in *Moraea fergusoniae*), sometimes villous abaxially. *Flowers* long-lived, variously coloured, usually with inner tepals 3-lobed with prominent central cusp or reduced to simple, hair-like cusps or absent (entire in a few species); stamens united in lower half or entirely, or united at base, rarely free or virtually so; style branches usually well developed with erect crests (reduced and crests vestigial in *M. worcesterensis*). *Capsules* ovoid-ellipsoid, usually exserted. *Basic chromosome number*  $x = 6$ .

10a. Sect. **Integres** Goldblatt & J.C.Manning, sect. nov. [Sect. *Thomasiae* Goldblatt in Annals of Kirstenbosch Botanic Garden 14: 138 (1986), invalid name]. Type species: *M. thomasiae* Goldblatt.

Plants often unbranched. *Foliage leaf* solitary. *Flowers* yellow, inner tepals spatulate, entire; filaments free or barely united at base.

135. *M. thomasiae* Goldblatt

10b. Sect. **Viusseuxia** (D.Delaroche) Goldblatt & J.C.Manning, comb. nov. *Viusseuxia* D.Delaroche: 31 (1766). Type species: as for subgenus.

Plants branched or not. *Foliage leaf* usually solitary (not *M. fergusoniae*). *Flowers* mostly blue to violet, pink, purple, white, rarely yellow; inner tepals often tricuspidate, hair-like, sometimes absent; filaments usually united in lower half, occasionally free or barely united at base.

136. *M. incurva* G.J.Lewis
137. *M. barkerae* Goldblatt
138. *M. lurida* Ker Gawl.
139. *M. cantharophila* Goldblatt & J.C.Manning
140. *M. insolens* Goldblatt
141. *M. worcesterensis* Goldblatt
142. *M. fergusoniae* L.Bolus
143. *M. unguiculata* Ker Gawl.
144. *M. rivulicola* Goldblatt & J.C.Manning
145. *M. algoensis* Goldblatt
146. *M. longiaristata* Goldblatt
147. *M. barnardii* L.Bolus
148. *M. debilis* Goldblatt
149. *M. lilacina* Goldblatt & J.C.Manning
150. *M. regalis* Goldblatt
151. *M. tricuspidata* Goldblatt
152. *M. deltoidea* Goldblatt & J.C.Manning
153. *M. bellendenii* Ker Gawl.
154. *M. trifida* R.C.Foster
155. *M. marionae* Baker
156. *M. dracomontana* Goldblatt
157. *M. modesta* Killick
158. *M. pubiflora* N.E.Br.
159. *M. brevistyla* (Goldblatt) Goldblatt
160. *M. vigilans* Goldblatt & J.C.Manning
161. *M. albicuspis* Goldblatt
162. *M. decipiens* Goldblatt & J.C.Manning
163. *M. helmei* Goldblatt & J.C.Manning



164. *M. mutila* (C.H.Bergius ex Eckl.) Goldblatt & J.C.Manning  
 165. *M. cuspidata* Goldblatt & J.C.Manning  
 166. *M. tripetala* (L.f.) Ker Gawl.  
 167. *M. ogamana* Goldblatt & J.C.Manning  
 168. *M. hainebachiana* Goldblatt & J.C.Manning  
 169. *M. amabilis* Diels  
 170. *M. grandis* Goldblatt & J.C.Manning

10c. Sect. **Villosae** Goldblatt & J.C.Manning, sect. nov. Type species: *M. villosa* (Ker Gawl.) Ker Gawl.

*Foliage leaf* and stem usually pilose or velvety abaxially (not *M. caeca*). *Flowers* variously coloured, large with outer tepal limbs exceeding claws, limbs rotund, as wide as or wider than long; inner tepals tricuspidate with central cusp long and trailing.

171. *M. aristata* (D.Delaroche) Asch. & Graeb.  
 172. *M. caeca* Goldblatt  
 173. *M. amissa* Goldblatt  
 174. *M. atropunctata* Goldblatt  
 175. *M. tulbaghensis* L.Bolus  
 176. *M. villosa* (Ker Gawl.) Ker Gawl.  
 177. *M. calcicola* Goldblatt  
 178. *M. loubseri* Goldblatt  
 179. *M. gigandra* L.Bolus

11. Subg. **Homeria** (Vent.) Goldblatt & J.C.Manning, comb. et stat. nov. *Homeria* Vent.: 2 (1808). Type species: *H. collina* (Thunb.) Salisb. (= *M. collina* Thunb.).

*Sessilistigma* Goldblatt: 156 (1984b). Type species: *S. radians* Goldblatt (= *Moraeca radians* (Goldblatt) Goldblatt).

Plants simple or few-branched; corm tunics of wiry, black fibres. *Foliage leaves* few to solitary. *Flowers* fugaceous or long-lived, yellow, beige or pink to orange, sometimes with dark markings; outer and inner tepals subequal, both whorls usually with nectar guides, claws as long as limbs or much shorter; stamens with filaments united entirely or free near apices (free in *M. radians*); style branches reduced with crests vestigial or absent. *Capsules* ovoid-ellipsoid to cylindric, included or exserted. *Basic chromosome number*  $x = 6$ .

11a. Sect. **Stipanthera** (Goldblatt) Goldblatt & J.C.Manning, comb. nov. *Homeria* sect. *Stipanthera* Goldblatt [*Stipanthera*] in Annals of the Missouri Botanical Garden 68: 426 (1981). Type species: *M. pallida* Baker.

*Leaf* solitary, clasping stem below. *Flowers* yellow (rarely pink); tepals with claws much shorter than limbs, clasping or forming a cup including base of filament column; stamens with filaments free near apices or fully united.

180. *M. cookii* L.Bolus  
 181. *M. pallida* Baker  
 182. *M. marlothii* L.Bolus  
 183. *M. reflexa* Goldblatt  
 184. *M. britteniae* (L.Bolus) Goldblatt

11b. Sect. **Flexuosae** Goldblatt in Annals of the Missouri Botanical Garden 69: 356 (1983, as 1982). Type

species: *M. flexuosa* Goldblatt (= *M. flexicaulis* Goldblatt).

*Homeria* sect. *Namaquanae* Goldblatt [*Namaquana*]: 425 (1981). Type species: *H. schlechteri* L. Bolus.

*Leaves* several, decreasing in size above. *Flowers* fugaceous, yellow; tepals with claws much shorter than limbs, clasping or forming a cup including base of filament column; stamens with filaments free near apices or  $\pm$  fully united.

185. *M. schlechteri* (L.Bolus) Goldblatt  
 186. *M. knersvlakensis* Goldblatt  
 187. *M. flexicaulis* Goldblatt

11b. Sect. **Homeria** (Vent.) Goldblatt in Novon 8: 374 (1998). Type species: *H. collina* (Thunb.) Salisb. (= *M. collina* Thunb.).

*Stem* straight or flexed. *Foliage leaves* several to one. *Flowers* fugaceous or lasting two days; tepal claws short and erect or long and forming a cup enclosing stamens; filaments usually united entirely (free in *M. radians*).

188. *M. cedarmonticola* Goldblatt  
 189. *M. autumnalis* (Goldblatt) Goldblatt  
 190. *M. ochroleuca* (Salisb.) Drapiez  
 191. *M. flaccida* Sweet  
 192. *M. collina* Thunb.  
 193. *M. pyrophila* Goldblatt  
 194. *M. minor* Eckl.  
 195. *M. longistyla* (Goldblatt) Goldblatt  
 196. *M. comptonii* (L.Bolus) Goldblatt  
 197. *M. elegans* Jacq.  
 198. *M. radians* (Goldblatt) Goldblatt  
 199. *M. bulbillifera* (G.J.Lewis) Goldblatt  
 200. *M. serratosyla* (Goldblatt) Goldblatt  
 201. *M. patens* (Goldblatt) Goldblatt  
 202. *M. lonisabolusiae* Goldblatt  
 203. *M. vallisbelli* (Goldblatt) Goldblatt  
 204. *M. flavescens* (Goldblatt) Goldblatt  
 205. *M. demissa* Goldblatt

11c. Sect. **Conantherae** (Goldblatt) Goldblatt & J.C.Manning, comb. nov. *Homeria* sect. *Conantherae* Goldblatt [*Conanthera*]: 427 (1981). Type species: *Homeria miniata* (Andrews) Sweet (= *M. miniata* Andrews).

*Stem* straight or flexed. *Foliage leaves* several to one. *Flowers* fugaceous, members of both whorls well developed and bearing nectar guides; tepal claws short, erect, forming a cup enclosing base of filaments; filaments united entirely; anthers parallel with stigmatic surfaces emerging between anthers.

206. *M. aspera* Goldblatt  
 207. *M. miniata* Andrews  
 208. *M. pendula* (Goldblatt) Goldblatt  
 209. *M. karooica* Goldblatt  
 210. *M. fenestrata* Goldblatt  
 211. *M. bifida* (L.Bolus) Goldblatt  
 212. *M. fragrans* Goldblatt  
 213. *M. fusconmontana* (Goldblatt) Goldblatt  
 214. *M. brachygyna* (Schltr.) Goldblatt

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# Review of chromosome cytology in *Moraea* (Iridaceae: Irideae): what chromosomes reveal about the evolution of the genus

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**Keywords:** chromosome rearrangement, dysploidy, polyploidy

## ABSTRACT

A review of the chromosome cytology of the African and Eurasian geophytic genus *Moraea* Mill. (currently 214 spp.); including 51 new counts, many for taxa poorly known cytologically or not counted before, that shows that 167 species, representing 78% of the total, have been counted from one or more populations. The inferred ancestral base number is  $x = 10$ . Polyploidy is relatively rare; available counts indicate that both Eurasian species are tetraploid, but that, among the sub-Saharan species, just nine species (less than 5%) are exclusively polyploid and an additional 15 (7%) have diploid and polyploid populations. Chromosome rearrangement leading to reduced base numbers has occurred in subg. *Polyanthes* ( $x = 10$ ), in which four sections have a base number of  $x = 6$ . Three subgenera, *Grandiflorae*, *Homeria* and *Vieusseuxia*, also have  $x = 6$ , but have different karyotypes. Several species and one subspecies are dysploid, all but one with haploid numbers lower than in related species, and are neodysploids. Except for *M. virgata* subsp. *karooica*, dysploidy is interpreted as descending. Fourteen species have diploid and polyploid populations, notably *M. crispa* (subg. *Polyanthes*) and *M. cookii* (subg. *Homeria*), in which the distribution of populations with  $2n = 12$ , 24 and 36 is correlated with geography. Seven species have euploid and dysploid populations at the diploid level and *M. inclinata* has populations with  $2n = 12$  and 22. Differences in chromosome number within species are not normally reflected in external morphology. Compared to most other genera of Iridaceae in sub-Saharan Africa, chromosome number and karyotype are unusually variable so that sampling of multiple populations of species is required to establish these characters. Although many species remain to be examined cytologically, those uncounted are mostly in the species-rich subg. *Grandiflorae* and subg. *Vieusseuxia*, both of which exhibit little variation in chromosome number and karyotype. Chromosome rearrangement and polyploidy appear to have been important in the early evolution of the genus as well as in recent speciation.

## INTRODUCTION

The cytology of the Afro-Mediterranean geophytic genus *Moraea* Mill. (currently 214 spp.) of Iridaceae, subfamily Iridoideae, has been the subject of extensive investigation because of the unusually wide variation in chromosome number and karyotype that closely correlate with morphological variation. *Moraea* also exhibits one of the most extensive dysploid reduction series in flowering plants. The correlation between karyology and morphology led Goldblatt (1976a) to propose an infrageneric classification using cytology as a major factor in circumscribing subgenera and sections. The circumscription of *Moraea* was subsequently expanded to include the related genera *Barnardiella* Goldblatt, *Galaxia* Thunb., *Gynandriris* Parl., *Hexaglottis* Vent., *Homeria* Vent. and *Roggeveldia* Goldblatt. These genera were reduced to synonymy in *Moraea* on the basis of inferred morphological, and in some instances cytological, synapomorphies with species groups within *Moraea* (Goldblatt 1998). A molecular DNA-based phylogenetic study of *Moraea* subsequently confirmed Goldblatt's conclusion that *Moraea* is paraphyletic without the inclusion of these genera, thus endorsing its expanded circumscription (Goldblatt *et al.* 2002). That study and a second, more extensive one (Schnitzler *et al.* 2011)

also showed that Goldblatt's (1976a) infrageneric classification of *Moraea* needed extensive revision. Although most of the more distinctive species clusters are monophyletic, subg. *Moraea* included disparate elements and required major revision. In addition, some species or species clusters did not fall in the subgenera or sections to which they had been assigned. Our new classification based on phylogenetic principles and integrating molecular and morphological data recognizes 11 subgenera (Goldblatt *et al.* 2013) and provides a framework for interpreting cytological evolution in the genus. Here we provide a review of chromosome cytology in *Moraea* following this new classification. We include 51 new chromosome reports, several for species known until now from a single count and five for species previously unknown cytologically. Chromosome numbers have now been reported for 167 of the 214 species of *Moraea* currently recognized, representing 78% of the genus, a significant albeit incomplete survey.

## MATERIALS AND METHODS

Data on chromosome numbers in *Moraea* were extracted from Goldblatt's (1971) review of the cytology of southern African Iridaceae and from indexes to plant chromosome numbers that included chromosome numbers published after that time (Moore 1974, 1977; Goldblatt 1981c, 1984c, 1985a, 1987a; Goldblatt & Johnson 1990, 1994, 1996, 2000, 2003, 2006, 2010). Counts are tabulated following the revised, phylogenetic infrageneric classification (Goldblatt *et al.* 2013), with species names corrected to reflect current nomenclature and taxonomy. Original sources were consulted for all counts.

We interpret patterns of change in chromosome number and karyotype in light of the plastid DNA-based

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phylogeny, also published in *Bothalia* 43(1), which includes a phylogenetic tree that may be consulted as companion to this review (Goldblatt *et al.* 2013). We then relate the patterns to established hypotheses for interpreting these phenomena by Stebbins (1950, 1971), Jones (1970) and Raven (1975). Briefly, polyploid sequences always proceed from lower to higher numbers by doubling. Stepwise changes, rather than doubling of base numbers are, we believe, largely descending in a process involving translocation of chromosome material to a second chromosome, accompanied by loss of a centromere, some heterochromatin and those genes associated with cell division. The process is here and throughout the text referred to as dysploidy. Descending dysploid reduction sometimes results in translocation of a long chromosome arm of an acrocentric chromosome to the short arm of another and loss of the centromere portion of the donor chromosome, resulting in a large metacentric chromosome and a lower base number, a process often called chromosome fusion or Robertsonian translocation. Translocation of the long chromosome arm of a short acrocentric chromosome to the distal end of the long arm of a second chromosome and loss of the centromere of the donor chromosome yields a longer, acrocentric chromosome.

### Original counts

For original counts, root tips of newly sprouted corms were harvested in mid-morning and prepared according to a root tip squash method described by Goldblatt & Takei (1993). Vouchers are housed at the Missouri Botanical Garden Herbarium (MO) and Compton Herbarium (NBG). Counts are based on samples of three to four individuals unless otherwise stated and, following widespread practice in plant cytology, are assumed to represent entire populations.

## RESULTS

### Chromosome number

The most parsimonious interpretation of the available data shows ancestral basic chromosome number in *Moraea* is  $x = 10$ . This was first established by outgroup comparison, where  $x = 10$  is the base number (and only chromosome base number) for the related genera *Bobartia* L., *Dietes* Salisb. ex Klatt and *Ferraria* Burm. ex Mill. (Goldblatt 1971, 1981c; Goldblatt & Takei 1997). Subsequent DNA sequence-based phylogenetic analyses (Goldblatt *et al.* 2002; Schnitzler *et al.* 2011; Goldblatt *et al.* 2013) are congruent with this hypothesis—species with base numbers of  $x = 10$  are consistently retrieved as ancestral to species with other base numbers.

A base of  $x = 10$  characterizes the monospecific subg. *Phumariaeae*, five (of eight) species counted in subg. *Viscirasosae*, and seven (of eight) species counted in subg. *Umbellatae* (Table 1). The three subgenera are collectively sister to the remaining species of *Moraea* [see phylogenetic tree in Goldblatt *et al.* (2013)]. Counts for all but two species are diploid,  $2n = 20$ , but the two counts for *M. margaretae* (subg. *Umbellatae*) are tetraploid,  $2n = 40$ . The single count for *M. linderi* is  $2n = 30$ , thus triploid, but only two individuals of this extremely rare species were available for study and it

seems likely that the species is normally diploid. Subgenera *Acaules*, *Monocephalae* and *Moraea* also have  $x = 10$ . Two species of subg. *Moraea* are dysploid: *M. indecora* has  $2n = 16$  and, as circumscribed at present, *M. papilionacea* has southern populations with  $2n = 18$  and a northern Cedarberg population has  $2n = 16$  (Goldblatt 1971; 1976a).

In subg. *Acaules*, *Moraea tricolor* has dysploid populations in the west of its range (three populations documented with  $2n = 18$ ), but two pink-flowered populations from the Caledon District (the eastern part of its range) have  $2n = 20$ . In *M. ciliata* two of ten counts, both from the Caledon District, are tetraploid,  $2n = 40$ ; and one population from Glenlyon, Nieuwoudtville, includes both euploid and dysploid individuals (Goldblatt 1976a). Based on available counts, these six subgenera together have 26 species exclusively diploid, one exclusively tetraploid, one heteroploid, two dysploid at the diploid level, and one (*M. tricolor*) with dysploid and euploid populations.

The specialized, acaulescent subg. *Galaxia*, with all but two of 17 species counted, has  $x = 9$ . This is the only base number in ser. *Galaxia* (Table 1) and also in the monospecific ser. *Unguiculatae* (sister to ser. *Eurystigma* and *Galaxia*). Ser. *Eurystigma*, in contrast, exhibits an extended dysploid series,  $n = 8, 7$ , and 6. *M. versicolor* of ser. *Eurystigma* has most populations with  $n = 8$  but populations from the northern Cape Peninsula have  $n = 7$ . *M. galaxia* (ser. *Galaxia*) is heteroploid, with most populations  $2n = 36$ , thus tetraploid, but one population in the eastern part of its range is diploid,  $2n = 18$ , and another from the northern end of its range has  $2n = 54$ , thus hexaploid. Three counts for *M. stagnalis* are also tetraploid,  $2n = 36$ . Counts for all members of ser. *Eurystigma* are at the diploid level except *M. citrina*, in which three populations counted are diploid with  $2n = 16$ , one is tetraploid and one dysploid with  $2n = 14$  (Goldblatt 1979a).

Subg. *Polyanthes*, now including several species previously assigned to subg. *Moraea* (Goldblatt 1976a) has  $x = 10$  in sects. *Deserticola* and *Serpentinae* (Table 1). The four remaining sections all have the derived base of  $x = 6$ . In the *M. fugax* complex (sect. *Deserticola*), *M. gracilenta* and *M. macrocarpa* have exclusively  $2n = 20$  (five populations counted) but races of *M. fugax* have  $n = 10, 9, 8, 7, 6$  and 5. Closely allied *M. filicaulis* (also treated as a subspecies of *M. fugax*), has diploid numbers of  $2n = 12$  and 10. As noted elsewhere (Goldblatt 1986b), this dysploid series in *M. fugax* is remarkable for a single species, albeit a variable one with distinct morphological races. Outgroup comparison compels us to interpret the series as descending. Significantly, populations of *M. fugax* with  $2n = 10$  have about the same genome size as species with  $2n = 20$  based on measurements of chromosome length (Goldblatt *et al.* 1986b; Goldblatt & Takei 1997). This independently supports our inference that the pattern in *M. fugax* represents descending dysploidy. An early count of  $2n = 28$  in *M. fugax* by Sakai (1952) must be seen as an error: most likely his study material was misidentified.

The remaining four sections of subg. *Polyanthes* (Table 1) have  $x = 6$ . Sect. *Polyanthes* has exclusively

Table 1.—Chromosome numbers in *Moraea* with collection data for new counts. Unless stated to the contrary, vouchers are at the Missouri Botanical Garden (MO). Herbarium acronyms are abbreviated according to Holmgren *et al.* (1990) and are indicated in parentheses after collection number. Subgenera and sections are arranged in phylogenetic sequence following in Goldblatt *et al.* (2013), but species are arranged alphabetically. For the sake of brevity, collection data for past counts are not included. Abbreviations: S. Africa = South Africa; E. Cape = Eastern Cape; KZN = KwaZulu-Natal, N. Cape = Northern Cape, W. Cape = Western Cape, n/v = no voucher.

Species	Diploid no. 2n (number of populations)	Collection data or reference for published counts
Subg. <i>Plumariae</i> Goldblatt & J.C.Manning		
<i>M. lugubris</i> (Salisb.) Goldblatt	20 (1)	(Goldblatt 1976a)
Subg. <i>Viscramosae</i> Goldblatt		
(uncounted: <i>M. simplex</i> Goldblatt & J.C.Manning; <i>M. vespertina</i> Goldblatt & J.C.Manning; <i>M. saldanensis</i> Goldblatt & J.C.Manning)		
<i>M. bubalina</i> Goldblatt	20 (1)	S. Africa, N. Cape, Soutpan road, <i>Goldblatt 7074</i>
<i>M. bituminosa</i> (L.f.) Ker Gawl.	20 (1)	(Goldblatt 1976a)
<i>M. elsiae</i> Goldblatt	20 (2)	(Goldblatt 1976a; Goldblatt & Takei 1997)
<i>M. inconspicua</i> Goldblatt	20 (1)	(Goldblatt 1976a, as <i>M. viscaria</i> (L. f.) Ker Gawl.
<i>M. viscaria</i> (L.f.) Ker Gawl.	20 (2)	(Goldblatt 1971; 1976a, as <i>M. odorata</i> G.J. Lewis)
Subg. <i>Umbellatae</i> Goldblatt & J.C.Manning		
(uncounted <i>M. intermedia</i> Goldblatt & J.C. Manning)		
<i>M. cooperi</i> Baker	20 (1)	(Goldblatt 1971)
<i>M. linderi</i> Goldblatt	30 (1)	S. Africa, W. Cape, Cold Bokkeveld, <i>Goldblatt 8031</i>
<i>M. longiflora</i> Ker Gawl.	20 (1)	S. Africa, N. Cape, Kamiesberg, <i>Goldblatt 4317</i>
<i>M. margaretae</i> Goldblatt	40 (2)	(Goldblatt 1976a)
<i>M. maximiliani</i> (Schltr.) Goldblatt	20 (1)	(Goldblatt 1980a, as <i>Rheome maximiliani</i> (Schltr.) Goldblatt)
<i>M. nana</i> (L.Bolus) Goldblatt	20 (3)	(Goldblatt 1987b, as <i>Hexaglottis nana</i> L. Bolus); S. Africa, N. Cape, Spektakel Mtns. <i>Goldblatt 6669</i> .
<i>M. umbellata</i> Thunb.	20 (1) 30 (3)	(Goldblatt 1987b, as <i>Rheome umbellata</i> (Thunb.) Goldblatt) (Goldblatt 1980a, 1987b, as <i>Rheome umbellata</i> (Thunb.) Goldblatt)
Subg. <i>Moraea</i>		
<i>M. garipeensis</i> Goldblatt	20 (1)	(Goldblatt 1986a then undocumented; Namibia), <i>Goldblatt 7153</i>
<i>M. gawleri</i> Spreng.	20, 24 (2) 20 (2)	(Goldblatt 1971—latter count now believed to be 20 + 4B) S. Africa, W. Cape, Hout Bay, <i>Goldblatt 4972</i> ; Swellendam to Bontebok Park, <i>Goldblatt s.n. n/v</i>
<i>M. indecora</i> Goldblatt	16 (1)	(Goldblatt 1986a then undocumented; S. Africa, W. Cape, <i>Goldblatt 3053</i> )
<i>M. namaquamontana</i> Goldblatt	20 (1)	(Goldblatt 1986a then undocumented; S. Africa, W. Cape, <i>Oliver et al. 627</i> )
<i>M. nubigena</i> Goldblatt	20 (1)	(Goldblatt 1986a then undocumented; S. Africa, W. Cape, <i>Goldblatt 4208</i> )
<i>M. papilionacea</i> (L.f.) Ker Gawl.	18 (3) 16 (1)	(Goldblatt 1971; 1976a) S. Africa, W. Cape, Cedarberg, <i>Goldblatt 5136</i>
<i>M. ramosissima</i> (L.f.) Ker Gawl.	20 (2)	(Sakai 1952; Goldblatt 1971)
<i>M. vegeta</i> L.	20 (3)	(Fernandes & Neves 1961; Goldblatt 1971 as <i>M. juncea</i> L.); S. Africa, W. Cape, Hout Bay, <i>Goldblatt 4973</i>
<i>M. vlokii</i> Goldblatt	20 (1)	(Goldblatt 1992)
Subg. <i>Galaxia</i> (Thunb.) Goldblatt		
Ser. <i>Galaxia</i>		
(uncounted: <i>M. vivuzela</i> J.C.Manning & Goldblatt)		
<i>M. albiflora</i> (G.J.Lewis) Goldblatt	18 (5)	(Goldblatt 1979a, as <i>G. albiflora</i> G.J. Lewis)
<i>M. angulata</i> Goldblatt	18(27) (1) 27 (1)	(Goldblatt 1979a, as <i>G. alata</i> Goldblatt)
<i>M. fugacissima</i> (L.f.) Goldblatt	15 (5) 16 (1)	(Goldblatt 1979a, as <i>G. fugacissima</i> (L.f.) Druce) (Goldblatt 1971, later corrected to 18)
<i>M. kamiesensis</i> Goldblatt	18 (1)	(Goldblatt 1979a, as <i>G. grandiflora</i> Andrews)
<i>M. luteoalba</i> (Goldblatt) Goldblatt	18 (2) 27 (1)	(Goldblatt 1979a, as <i>G. luteoalba</i> Goldblatt)
<i>M. galaxia</i> Goldblatt & J.C.Manning (all as <i>Galaxia ovata</i> Thunb.)	18 (2) 36 (5) 54 (1) 16 (1)	(Goldblatt 1979a) (Goldblatt 1984a) (Goldblatt 1971, later corrected to 18)
<i>M. pilifolia</i> Goldblatt	18 (2)	(Goldblatt 1979a, as <i>G. ciliata</i> Pers.)
<i>M. stagnalis</i> (Goldblatt) Goldblatt	36 (3)	(Goldblatt 1979a, as <i>G. stagnalis</i> Goldblatt)
Ser. <i>Eurystigma</i> (Goldblatt) Goldblatt		



Species	Diploid no. 2n (number of populations)	Collection data or reference for published counts
(uncounted: <i>M. fenestralis</i> (Goldblatt & E.G.H.Oliver) Goldblatt)		
<i>M. barnardiella</i> Goldblatt	16 (4)	(Goldblatt 1979a, 1984a, as <i>G. barnardii</i> Goldblatt)
<i>M. citrina</i> (G.J.Lewis) Goldblatt	16 (3)	(Goldblatt 1971, 1979a, as <i>G. citrina</i> G. J. Lewis)
	34 (1)	
	14 (1)	
<i>M. melanops</i> Goldblatt & J.C. Manning	16 (1)	(Goldblatt 1979a, as <i>G. barnardii</i> Goldblatt)
<i>M. minima</i> Goldblatt	12 (1)	Goldblatt 1984a, as <i>G. parva</i> Goldblatt)
<i>M. variabilis</i> (G.J.Lewis) Goldblatt	14 (5)	(Goldblatt 1979a, as <i>G. variabilis</i> G. J. Lewis)
<i>M. versicolor</i> (Salisb. ex Klatt) Goldblatt	16 (3)	(Goldblatt 1979a, as <i>G. versicolor</i> Salisb. ex Klatt)
	14 (3)	
Ser. <i>Unguiculatae</i> Goldblatt & J.C.Manning		
<i>M. kamiesmontana</i> (Goldblatt) Goldblatt	18 (1)	(Goldblatt 1984a, as <i>G. kamiesmontana</i> Goldblatt)
Subg. <i>Macrocephalae</i>		
(uncounted: <i>M. vallisavium</i> Goldblatt)		
<i>M. angusta</i> (Thunb.) Ker Gawl.	20 (2)	(Goldblatt 1971; Goldblatt & Takei 1997)
<i>M. anomala</i> G. Lewis	20 (1)	(Goldblatt & Takei, 1997)
<i>M. neglecta</i> G.J. Lewis	20 (2)	(Goldblatt 1971, 1976a; Goldblatt & Takei 1997)
Subg. <i>Acanthes</i>		
(uncounted: <i>M. longipes</i> Goldblatt & J.C. Manning)		
<i>M. ciliata</i> (L.f.) Ker Gawl.	20 (7)	(Goldblatt 1971, 1976a; Johnson & Brandham 1997); S. Africa, W. Cape, Cold Bokkeveld, <i>Goldblatt s.n.</i> n/v; Nardouwsberg, <i>Goldblatt 2195</i> ;
		Cedarberg, Middelberg, <i>Goldblatt 5131</i>
	20, 18	(Goldblatt 1976a)
	40 (2)	(Goldblatt 1976a); S. Africa, W. Cape, Bredasdorp Poort, <i>Goldblatt 6933</i>
<i>M. falcifolia</i> Klatt	20 (2)	(Goldblatt 1976a)
<i>M. macronyx</i> G.J.Lewis	20 (2)	(Goldblatt 1971; 1976a)
<i>M. tricolor</i> Andrews	18 (3)	(Goldblatt 1976a, as <i>M. ciliata</i> ); S. Africa, W. Cape, Camphill Village road, <i>Goldblatt 2178</i> ; Tinnie Versfeld Reserve, Darling, <i>Goldblatt s.n.</i> n/v)
	20 (2)	S. Africa, W. Cape, Drayton Siding, <i>Goldblatt 2516</i> ; W. Cape, near Esel-jacht Pass, <i>Goldblatt s.n.</i> n/v
Subg. <i>Polyanthes</i> (Goldblatt) Goldblatt & J.C.Manning		
Sect. <i>Serpentinae</i> Goldblatt & J.C.Manning		
<i>M. serpentina</i> Baker	20 (4)	(Goldblatt 1971, as <i>M. framesii</i> L. Bolus; Goldblatt 1976a)
<i>M. tortilis</i> Goldblatt	20 (1)	(Goldblatt 1976a)
Sect. <i>Deserticola</i>		
<i>M. bolusii</i> Baker	20 (1)	(Goldblatt 1976a)
<i>M. filicanlis</i> Baker	12 (4)	(Goldblatt 1971 as <i>M. diphylla</i> Baker; 1980b as <i>M. fugax</i> subsp. <i>filicanlis</i> (Baker) Goldblatt)
	10 (3)	
<i>M. fugax</i> (D.Delaroche) Jacq.	20 (3)	(Goldblatt 1971; 1986b as <i>M. fugax</i> or subsp. <i>fugax</i> )
	18 (7)	
	16 (1)	
	14 (3)	
	12 (4)	
	10 (8)	
<i>M. gracilentia</i> Goldblatt	20 (2)	(Goldblatt 1976a, as <i>M. fugax</i> var. <i>gracilis</i> Baker; 1986b)
<i>M. granitcola</i> Goldblatt	20 (1)	(Goldblatt 1986c)
<i>M. herrei</i> (L. Bolus) Goldblatt	20 (3)	(Goldblatt 1976c; Goldblatt & Takei 1997) (as <i>Barnardiella spiralis</i> (N.E.Br.) Goldblatt)
<i>M. hexaglottis</i> Goldblatt	20 (1)	(Goldblatt 1986c)
<i>M. macrocarpa</i> Goldblatt	20 (3)	(Goldblatt 1986c)
<i>M. macgregorii</i> Goldblatt	20 (1)	(Goldblatt 1976a)
<i>M. namibensis</i> Goldblatt	20 (1)	(Goldblatt & Takei 1997)
<i>M. rigidifolia</i> Goldblatt	20 (1)	(Goldblatt 1986c)
<i>M. saxicola</i> Goldblatt	20 (1)	(Goldblatt 1976a)
	20 (1)	S. Africa, N. Cape, Garies-Bitterfontein, <i>Goldblatt 4257</i>

Species	Diploid no. 2n (number of populations)	Collection data or reference for published counts
Sect. <i>Hexaglottis</i> (Vent.) Goldblatt		
<i>M. brevītuba</i> (Goldblatt) Goldblatt	24 (1)	(Goldblatt 1987b, as <i>H. brevītuba</i> Goldblatt)
<i>M. lewisiae</i> (Goldblatt) Goldblatt	12 (4)	(Goldblatt 1987b, as <i>H. lewisiae</i> Goldblatt)
<i>M. longifolia</i> (Jacq.) Pers.	24 (2)	(Goldblatt 1987b, as <i>H. longifolia</i> (Jacq.) Salisb.)
<i>M. namaquana</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1987b, as <i>H. namaquana</i> Goldblatt)
<i>M. riparia</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1987b, as <i>H. riparia</i> Goldblatt)
<i>M. virgata</i> Jacq. subsp. <i>virgata</i>	12 (5)	(Goldblatt 1987b, as <i>H. virgata</i> (Jacq.) Sweet)
	10 (4)	(Goldblatt 1971, 1987b)
subsp. <i>karooica</i> (Goldblatt) Goldblatt	14 (2)	(Goldblatt 1987b, as <i>H. virgata</i> subsp. <i>karooica</i> Goldblatt)
Sect. <i>Polyanthes</i>		
(uncounted: <i>M. tanquana</i> Goldblatt & J.C.Manning)		
<i>M. bipartita</i> L. Bolus	12 (3)	(Goldblatt & Takei 1997); S. Africa, W. Cape, near Lemoenshoek, <i>Goldblatt 4187</i> ; Attaquas Kloof, <i>Vlok s.n</i>
<i>M. deserticola</i> Goldblatt	12 (1)	(Goldblatt & Takei 1997)
<i>M. polyanthos</i> Thunb.	12 (8)	(Goldblatt 1971, as <i>Homeria lilacina</i> L. Bolus); (Goldblatt 1980a; Goldblatt & Takei 1997); S. Africa, W. Cape, Little Brak River, <i>Goldblatt 4919</i> ; near Albertinia, <i>Goldblatt 4954</i>
<i>M. polystachya</i> (L.f.) Ker Gawl.	12 (5)	(Riley 1962; Goldblatt 1971, Goldblatt 1976a)
<i>M. speciosa</i> (L. Bolus) Goldblatt	12 (2)	Goldblatt 1980a)
<i>M. venenata</i> Dinter	12 (1)	(Goldblatt 1976a, as <i>M. polystachya</i> , <i>Tölken 3985</i> (BOL)).
Sect. <i>Pseudospicatae</i> Goldblatt & J.C.Manning		
(uncounted: <i>M. afro-orientale</i> Goldblatt, <i>M. iringensis</i> Goldblatt, <i>M. pearsonii</i> Goldblatt & J.C.Manning, <i>M. marginata</i> J.C.Manning & Goldblatt)		
<i>M. alpina</i> Goldblatt	12 (1)	Lesotho, top of Sani Pass, <i>Hilliard &amp; Burt 8773</i> (E)
<i>M. callista</i> Goldblatt	12 (2)	(Goldblatt & Takei 1997)
<i>M. carsonii</i> Baker	12 (2)	(Goldblatt 1976a; Goldblatt & Takei 1997)
<i>M. crispa</i> Thunb.	12 (6)	(Goldblatt 1980a); S. Africa, W. Cape, near Beaufort West <i>Esterhuysen s.n.</i> ; N. Cape, Roggeveld, Quaggasfontein, <i>Goldblatt s.n.</i>
	24 (4)	(Goldblatt 1980a); S. Africa, W. Cape, Cedarberg, Krom R., <i>Goldblatt 5126</i> ; Cedarberg, Eikeboom, <i>Goldblatt 5128</i> ; N. Cape, near Nieuwoudville, <i>Goldblatt s.n. n/v</i>
	36 (1)	S. Africa, W. Cape, near Gydo Pass, <i>Goldblatt 5124</i>
<i>M. elliotii</i> Baker	12 (2)	(Lewis 1966; Goldblatt 1976a)
	24 (1)	(Goldblatt 1976a)
<i>M. exiliflora</i> Goldblatt	12 (1)	S. Africa, W. Cape, <i>Esterhuysen 36122</i>
<i>M. fistulosa</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1979b, as <i>Roggevelidia fistulosa</i> Goldblatt)
<i>M. inclinata</i> Goldblatt	12 (1)	S. Africa, E. Cape, Mhlahlane, <i>Goldblatt 7595</i>
	22 (1)	S. Africa, KZN, Cobham Forest Station, <i>Hilliard &amp; Burt 9694</i> (E)
<i>M. monticola</i> Goldblatt	24 (1)	(Goldblatt 1992, as <i>Roggevelidia montana</i> Goldblatt)
<i>M. natalensis</i> Baker	12 (2)	(Lewis 1966, as <i>M. erici-rosenii</i> Fries); Zimbabwe, <i>Goldblatt 5935</i>
<i>M. pseudospicata</i> Goldblatt	12 (1)	(Goldblatt 1986c)
<i>M. stricta</i> Baker	24 (2)	(Goldblatt 1971, as <i>M. trita</i> N.E. Br.); S. Africa, Gauteng, Blyvooruitzicht, <i>Goldblatt s.n. no voucher</i>
	36 (1)	(Goldblatt 1976a)
	48 (1)	(Goldblatt 1977)
	60 (1)	Malawi, Nyika Plateau, <i>Pawek 12942</i>
<i>M. thomsonii</i> Baker	12 (2)	(Chimphamba 1974); S. Africa, Mpumalanga, Mt. Sheba, <i>Davidson s.n. (J)</i>
<i>M. verecunda</i> Goldblatt	12 (1)	S. Africa, N. Cape, Nieuwoudville, <i>Holmes s.n.</i>
Sect. <i>Gynandris</i>		
(uncounted: <i>M. contorta</i> Goldblatt)		
<i>M. australis</i> Goldblatt	12 (1)	(Goldblatt 1980b, as <i>G. australis</i> Goldblatt)
<i>M. cedarmontana</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980b, as <i>G. cedarmontana</i> Goldblatt)
<i>M. hesperantha</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980b, as <i>G. hesperantha</i> Goldblatt)
<i>M. mediterranea</i> Goldblatt	24 (4)	(Goldblatt 1980b, as <i>G. monophylla</i> Boiss. & Heldr. ex Klatt )
<i>M. pritzeliana</i> Diels	12 (3)	(Goldblatt 1971; 1980b, as <i>G. pritzeliana</i> (Diels) Goldblatt)
<i>M. setifolia</i> (L.f.) Druce	12 (4)	(Goldblatt 1971; 1980b, as <i>G. setifolia</i> (L.f.) R.C.Foster)
<i>M. simulans</i> Baker	24 (1)	(Goldblatt 1980b, as <i>G. simulans</i> (Baker) R.C.Foster)
	36 (1)	
<i>M. sisyrinchium</i> (L.) Ker Gawl.	24 (19)	(Goldblatt 1980b and references therein, as <i>G. sisyrinchium</i> (L.) Parl.)

Species	Diploid no. 2n (number of popu- lations)	Collection data or reference for published counts
Subg. <i>Vieusseuxia</i> (D.Delaroche) Baker		
Sect. <i>Integres</i> Goldblatt & J.C.Manning		
<i>M. thomasiae</i> Goldblatt	12 (1)	(Goldblatt 1976a)
Sect. <i>Vieusseuxia</i> (D.Delaroche) Goldblatt & J.C.Manning		
(uncounted: <i>M. albicuspa</i> Goldblatt; <i>M. cantharophila</i> Goldblatt & J.C.Manning; <i>M. deltoidea</i> Goldblatt & J.C.Manning; <i>M. decipiens</i> Goldblatt & J.C.Manning; <i>M. dracomontana</i> Goldblatt; <i>M. hainebachiana</i> Goldblatt & J.C.Manning; <i>M. helmei</i> Goldblatt & J.C.Manning; <i>M. lilacina</i> Goldblatt & J.C.Manning; <i>M. longiaristata</i> Goldblatt; <i>M. modesta</i> Killick; <i>M. ogamana</i> Goldblatt & J.C.Manning; <i>M. pubiflora</i> N.E.Br.; <i>M. rivulicola</i> Goldblatt & J.C.Manning; <i>M. vigilans</i> Goldblatt & J.C.Manning)		
<i>M. algoensis</i> Goldblatt	12 (3)	(Goldblatt 1976a); S. Africa, W. Cape, Karoo Garden, Worcester, <i>Olivier 138</i> (NBG); E. Cape, near Hankey, <i>Goldblatt 4934</i>
<i>M. amabilis</i> Diels	12 (4)	(Goldblatt 1971 as <i>M. tripetala</i> ; Goldblatt & Manning 2012)
<i>M. aristata</i> (D.Delaroche) Asch. & Graebn.	12 (1)	(Goldblatt 1976a)
<i>M. atropunctata</i> Goldblatt	12 (1)	(Goldblatt 1982)
<i>M. barkerae</i> Goldblatt	12 (1)	(Goldblatt 1976b)
<i>M. barnardii</i> L.Bolus	12 (1)	(Goldblatt 1976a)
<i>M. bellendenii</i> Ker Gawl.	12 (1)	(Goldblatt 1971)
<i>M. brevistyla</i> (Goldblatt) Goldblatt	12 (1)	S. Africa, KZN, Giants Castle, <i>Goldblatt &amp; Manning s.n.</i>
<i>M. caeca</i> Goldblatt	12 (1)	(Goldblatt 1976a)
<i>M. cuspidata</i> Goldblatt & J.C.Manning	12 (1)	(Goldblatt 1976a, as <i>M. tripetala</i> )
<i>M. debilis</i> Goldblatt	12 (2)	(Goldblatt 1976a); S. Africa, W. Cape, Caledon District, <i>Goldblatt 2495</i>
<i>M. fergusoniae</i> L.Bolus	20 (1)	(Goldblatt 1971—evidently for another species)
	12 (4)	(Goldblatt & Takei 1997)
<i>M. grandis</i> Goldblatt & J.C.Manning	12 (2)	(Goldblatt 1976a; Goldblatt & Manning 2012)
<i>M. incurva</i> G. Lewis	12 (1)	(Goldblatt & Takei 1997)
<i>M. insolens</i> Goldblatt	12 (1)	(Goldblatt 1976a)
<i>M. lurida</i> Ker Gawl.	12 (3)	(Goldblatt 1971; 1976a)
<i>M. marionae</i> Baker	12 (1)	S. Africa, Mpumalanga, Mt. Sheba, <i>Davidson 3227</i> (J)
<i>M. mutila</i> (C.H.Bergius ex Eckl.) Goldblatt & J.C.Manning	12 (2)	(Goldblatt & Manning 2012)
<i>M. tricuspidata</i> Goldblatt	12 (1)	(Goldblatt 1976a)
	24 (4)	(Goldblatt 1976a); S. Africa, E. Cape, Humansdorp, <i>Goldblatt 4928</i> ; near Grahamstown, <i>Goldblatt 5129</i> ; W. Cape, Cedarberg, near Eikeboom, <i>Goldblatt 5129</i>
<i>M. trifida</i> R.C.Foster	12 (1)	(Goldblatt 1986a)
<i>M. tripetala</i> Goldblatt	12 (5)	(Goldblatt 1976a; Goldblatt & Manning 2012)
<i>M. unguiculata</i> Ker Gawl.	12 (6)	(Goldblatt 1976a, as <i>M. tenuis</i> Ker Gawl.; Goldblatt & Takei 1997); S. Africa, N. Cape, near Middelpoos, <i>Goldblatt 6124</i> ; W. Cape, road to Jonas Kop, <i>Goldblatt 5865</i>
<i>M. worcesterensis</i> Goldblatt	12 (1)	(Goldblatt 1986c)
Sect. <i>Villosae</i> Goldblatt & J.C.Manning		
<i>M. calcicola</i> Goldblatt	12 (1)	(Goldblatt 1982)
<i>M. gigandra</i> L.Bolus	12 (1)	(Goldblatt 1976a)
<i>M. loubseri</i> Goldblatt	12 (1)	(Goldblatt 1976a)
<i>M. tulbaghensis</i> L.Bolus	24 (1)	(Goldblatt 1976a)
	12 (2)	(Goldblatt & Takei 1997); (Goldblatt 1976a, as <i>M. neopavonia</i> R.C.Foster)
<i>M. villosa</i> (Ker Gawl.) Ker Gawl.		
subsp. <i>villosa</i>	24 (2)	(Goldblatt 1971))
subsp. <i>elandsmontana</i> Goldblatt	12 (1)	(Goldblatt 1982)
Subg. <i>Grandiflora</i>		
(uncounted: <i>M. angolensis</i> Goldblatt, <i>M. ardesiaca</i> Goldblatt, <i>M. bahundana</i> Goldblatt, <i>M. bovonei</i> R.C.Foster, <i>M. brevifolia</i> Goldblatt, <i>M. carnea</i> Goldblatt, <i>M. clavata</i> Goldblatt, <i>M. hiemalis</i> Goldblatt, <i>M. inyangani</i> Goldblatt, <i>M. muddii</i> N.E.Br., <i>M. reticulata</i> Goldblatt, <i>M. robusta</i> (Goldblatt) Goldblatt, <i>M. textilis</i> Baker, <i>M. unibracteata</i> Goldblatt, <i>M. upembana</i> Goldblatt, <i>M. verdickii</i> De Wild.)		
<i>M. alticola</i> Goldblatt	12 (1)	(Goldblatt 1976a)
<i>M. bella</i> Harms	12 (1)	(Goldblatt & Takei 1997)
<i>M. galpinii</i> (Baker) N.E.Br.	12 (1)	S. Africa, Mpumalanga, Mt. Sheba, <i>Murday 1159</i> (J)
<i>M. graminicola</i> Oberm.	12 (1)	(Goldblatt 1971)
	12 (1)	S. Africa, KZN, Cobham, <i>Hilliard &amp; Burtt 9420A</i> (E)



Species	Diploid no. 2n (number of populations)	Collection data or reference for published counts
<i>M. huttonii</i> (Baker) Oberm.	12 (3)	(Goldblatt 1976a); S. Africa, KZN, Umzimonti Valley Hilliard & Burt 9405 (E); Free State, NE of Van Reenen, Hilliard & Burt 9405 (E)
<i>M. macrantha</i> Baker	12 (3)	(Goldblatt 1977; 1976a as <i>M. textilis</i> Baker)
<i>M. moggii</i> N.E.Br.	12 (1)	(Goldblatt 1971)
<i>M. schimperii</i> (Hochst.) Pic.Serm.	12 (5)	(Goldblatt 1976a; Goldblatt & Takei 1997)
<i>M. spathulata</i> (L.f.) Klatt	12 (6)	(Riley 1962; Lewis 1966, as <i>M. spathacea</i> ; Goldblatt 1971)
<i>M. tanzanica</i> Goldblatt	12 (1)	(Goldblatt 1977)
<i>M. aff. ventricosa</i> Baker	12 (1)	(Goldblatt 1977)
Subg. <i>Homeria</i>		
<i>M. aspera</i> Goldblatt	12 (2)	(Goldblatt 1980a, as <i>H. spiralis</i> L. Bolus)
<i>M. autumnalis</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1981b, as <i>H. autumnalis</i> Goldblatt)
<i>M. bifida</i> (L.Bolus) Goldblatt	12 (4) 12 + 4B (1) 24 (1)	(Goldblatt 1980a, as <i>H. bifida</i> L. Bolus)
<i>M. brachygyna</i> (Schltr) Goldblatt	12 (3)	(Goldblatt 1971; 1980a, as <i>H. brachygyna</i> Schltr.)
<i>M. britteniae</i> (L.Bolus) Goldblatt	12 (1) 24 (1)	(Goldblatt 1980a, as <i>H. britteniae</i> L. Bolus)
<i>M. bulbifera</i> (G.J.Lewis) Goldblatt	12 (5) 12 + 1B (1) 18 (1) 24 (1)	(Goldblatt 1980a, as <i>H. bulbifera</i> G.J. Lewis)
<i>M. cedarmonticola</i> Goldblatt	12 (3)	(Goldblatt 1980a; 1981b, as <i>H. cedarmontana</i> Goldblatt)
<i>M. collina</i> Thunb.	24 (11)	(Goldblatt 1980a, as <i>H. collina</i> (Thunb.) Salisb.)
<i>M. comptonii</i> (L.Bolus) Goldblatt	12 (5)	(Goldblatt 1980a, as <i>H. comptonii</i> L. Bolus)
<i>M. cookii</i> (L.Bolus) Goldblatt	12 (2) 24 (1) 24 (3) 36 (2)	(Goldblatt 1980a; 1992, as <i>H. cookii</i> L. Bolus) (Goldblatt 1971, as <i>H. pallida</i> Baker) (Goldblatt 1980a)
<i>M. demissa</i> Goldblatt	10 (2) 9 (5) 8 (1)	(Goldblatt 1980a; 1981b, as (as <i>H. tenuis</i> Schltr.) (Goldblatt 1981b)
<i>M. elegans</i> Jacq.	12 (3)	(Goldblatt 1980a, as <i>H. elegans</i> (Jacq.) Sweet)
<i>M. fenestrata</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980a, as <i>H. fenestrata</i> Goldblatt)
<i>M. flaccida</i> Sweet	24 (2) 36 (7)	(Goldblatt 1980a; 1992, as <i>H. flaccida</i> (Sweet) Steud.)
<i>M. flavescens</i> (Goldblatt) Goldblatt	9 (2)	(Goldblatt 1980b, as <i>H. flavescens</i> Goldblatt)
<i>M. flexicaulis</i> Goldblatt	12 (1)	(Goldblatt 1982, as <i>Moraea flexuosa</i> Goldblatt)
<i>M. fragrans</i> Goldblatt	12 (2)	(Goldblatt 1980a, as <i>H. odorata</i> L. Bolus).
<i>M. fuscomontana</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1981b, as <i>H. fuscomontana</i> Goldblatt)
<i>M. karooica</i> Goldblatt	12 (3)	(Goldblatt 1980a, as <i>H. tricolor</i> G.J.Lewis)
<i>M. knersvlaktensis</i> Goldblatt	12 (1)	(Goldblatt 1980a, as <i>H. ramosissima</i> Schltr.)
<i>M. longistyla</i> (Goldblatt) Goldblatt	12 (6)	(Goldblatt 1980a, as <i>H. longistyla</i> Goldblatt)
<i>M. louisabohusiae</i> Goldblatt	12 (1)	(Goldblatt 1981b, as <i>H. bolusiae</i> Goldblatt)
<i>M. marlothii</i> (L.Bolus) Goldblatt	24 (1)	(Goldblatt 1980a, as <i>H. marlothii</i> L. Bolus)
<i>M. miniata</i> Andrews	12 (10) 24 (1)	(Goldblatt 1980a; 1981b, as <i>H. miniata</i> (Andrews) Sweet)
<i>M. minor</i> Eckl.	12 (7)	(Goldblatt 1980a; 1992, as <i>H. minor</i> (Eckl.) Goldblatt)
<i>M. ochroleuca</i> (Salisb.) Drapiez	12 (2) 24 (2) 24 + 2–3B (1)	(Goldblatt 1980a, as <i>H. ochroleuca</i> Salisb.)
<i>M. patens</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1981b, as <i>H. patens</i> Goldblatt)
<i>M. pallida</i> (Baker) Goldblatt	12 (2)  8 (4)	(Goldblatt 1971, as <i>H. glauca</i> (Wood & Evans) N.E.Br. and <i>H. pura</i> N.E. Br.) (Goldblatt 1981b as <i>H. pallida</i> Baker)
<i>M. pendula</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1980a, as <i>H. pendula</i> Goldblatt)
<i>M. pyrophila</i> Goldblatt	12 (2) 24 (1)	(Goldblatt 1981b; 1992 as <i>H. galpinii</i> L. Bolus) (Goldblatt 1980a, as <i>H. galpinii</i> L. Bolus)
<i>M. radians</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1984b, as <i>Sessilistigma radians</i> Goldblatt)
<i>M. reflexa</i> Goldblatt	12 (1)	(Goldblatt & Takei 1997 as <i>H. hantamensis</i> Goldblatt & J.C.Manning)
<i>M. schlechteri</i> (L.Bolus) Goldblatt	12 (5)	(Goldblatt 1980a; 1992, as <i>H. schlechteri</i> L. Bolus)
<i>M. serratosyla</i> (Goldblatt) Goldblatt	12 (1)	(Goldblatt 1992, as <i>H. serratosyla</i> Goldblatt)
<i>M. vallisbelli</i> (Goldblatt) Goldblatt	12 (2)	(Goldblatt 1980a, as <i>H. vallisbelli</i> Goldblatt)

$2n = 12$  in six (of seven) species counted. In sect. *Hexaglottis*, four of the six species are diploid,  $2n = 12$ . The remaining two species, *Moraea brevifolia* and the autogamous *M. longifolia*, are polyploid,  $2n = 24$  (Goldblatt 1987b as *Hexaglottis*). Among the diploid species of the section, the widespread *M. virgata* subsp. *virgata* has  $2n = 12$  over most of its range but  $2n = 10$  in the immediate southwestern Cape populations, these evidently derived from the ancestral  $x = 6$  for the section. Subsp. *karooica* of *M. virgata* is evidently also dysploid but has  $2n = 14$  in two populations counted (of three known at present). Two very small chromosomes account for the extra pair. The pattern in sect. *Gynandriis* is more complex (Table 1). The two Mediterranean–Middle Eastern species, *M. sisyrinchium* and *M. mediterranea*, are tetraploid,  $2n = 24$ , for the many populations counted (at least 19 records for *M. sisyrinchium*) (Goldblatt 1980b), and the southern African *G. simulans* is evidently also polyploid, based on two populations sampled, one  $2n = 24$  and the other  $2n = 36$ . Counts for five of the remaining six southern African species, all from the winter-rainfall region of the subcontinent, are exclusively diploid,  $2n = 12$ , but *M. contorta* remains uncounted.

Largest section of subg. *Polyanthes*, sect. *Pseudospicatae* with 13 of 18 species counted, has nine species exclusively diploid, all  $2n = 12$ , and two, *M. elliptica* and *M. inclinata*, with diploid and tetraploid populations (Table 1). The latter has  $2n = 22$  in the one polyploid population so far recorded, thus hypopolyploid. The widespread *M. stricta*, the range of which extends from Stutterheim in Eastern Cape, South Africa to Ethiopia, has southern populations tetraploid and hexaploid,  $2n = 24, 48$ , and a population in Malawi, pentaploid,  $2n = 60$ . Lastly, the comparatively widespread *M. crispa* has diploid, tetraploid and hexaploid populations, all based on  $n = 6$ . The six Great Karoo and Roggeveld populations sampled are diploid, four Cedarberg populations are tetraploid, and the single Cold Bokkeveld population, the southernmost sampled, is hexaploid, thus  $2n = 36$ . The only count for *M. uonticola* is tetraploid, thus  $2n = 24$ , in one of its two known populations.

For subg. *Polyanthes* as a whole, 34 (77%) of the species counted are exclusively diploid (including diploid level dysploids), seven (16%) are exclusively polyploid, and three (7%) have diploid and polyploid populations.

The remaining subgenera, *Grandiflora*, *Homeria* and *Viesseuxia* all have  $x = 6$  (Table 1). Although the molecular phylogeny (see phylogenetic tree in Goldblatt *et al.* 2013) retrieves them as possibly sharing a common ancestor (with weak statistical support), each has a different karyotype, suggesting that  $x = 6$  may have been achieved independently in each. The majority of species are diploid. For subg. *Grandiflora*, cytologically least well known of the subgenera, 11 of 28 species have been counted: all are diploid,  $2n = 12$ , and have an almost identical karyotype (Goldblatt 1971; Goldblatt & Takei 1997). In subg. *Viesseuxia*, 28 of 42 species are known from at least one count. Of these 25 are exclusively diploid and just three, *M. tricuspidata*, *M. tulbaghensis* and *M. villosa*, have diploid and tetraploid populations. No species is exclusively polyploid.

The cytology of subg. *Homeria* is particularly interesting for its diversity: 21 of the 35 species (all counted)

are exclusively diploid with  $2n = 12$ . Dysploid reduction at the diploid level has been documented in *Moraea pallida*, which has its easternmost populations diploid,  $2n = 12$ , and the western populations  $2n = 8$ . The latter are complex heterozygotes forming chromosome rings at meiosis (Goldblatt 1980c). In western South Africa, *M. demissa* has  $2n = 10, 9$  and 8; and the only number so far known for *M. flavescens* (two populations sampled) is  $2n = 9$ . These last two species, like unrelated *M. pallida*, are also complex heterozygotes, forming various patterns of chromosome rings at meiosis (Goldblatt 1986c). Both are autogamous and produce full capsules of normal-looking viable seeds. Seven species, *M. bifida*, *M. britteniae*, *M. bulbifera*, *M. cookii*, *M. miniata*, *M. ochroleuca* and *M. pyrophila*, have diploid and tetraploid populations (just one each of the several populations counted for *M. bifida* and *M. miniata*). The particularly widespread *M. cookii* has diploid, tetraploid and hexaploid populations and a pattern with a clear geographical component, with diploids occurring in the Western Karoo, tetraploids in the mountains of the Great Karoo, and hexaploids in the interior mountains of Western Cape. *M. flaccida* has both tetraploid and hexaploid populations and several counts for *H. collina* and the only one for *M. marlothii* are tetraploid,  $2n = 24$ . Thus on available data, only three (8%) of the 35 species of subg. *Homeria* counted, are exclusively polyploid.

#### Genome size

Chromosomes of all *Moraea* species, and most other members of Iridoideae, are relatively large compared with those of other subfamilies of Iridaceae (Goldblatt 1971; Goldblatt & Takei 1997), directly reflecting larger genome sizes. Total DNA per cell in most diploid species is in the range 15–27 pg (Goldblatt *et al.* 1984c) using the correction factor determined by Goldblatt & Takei (1997). *Diets* and *Ferraria*, the other African members of tribe Irideae (to which *Moraea* belongs), have a similar genome size and comparably large chromosomes. In *Moraea*, chromosomes of subg. *Galaxia* are the smallest in the genus (Goldblatt 1971), evidently a derived condition: the one diploid species sampled, *M. fugacissima*, has just 4.8 pg per cell, somewhat less than half that in other subgenera. In subg. *Viesseuxia*, species of sect. *Villosae* have particularly large chromosomes and a genome size of  $\pm 27$  pg in the diploid *M. calcicola* and  $\pm 54$  pg in polyploid samples of *M. tulbaghensis* and *M. villosa*. The single species of sect. *Viesseuxia* sampled, *M. unguiculata*, has a genome size of  $\pm 19.7$  pg, thus consistent with most other subgenera. Genome size in subg. *Grandiflorae* is evidently the largest in the genus, as determined by chromosome size alone. Comparing chromosome volume (not length), Goldblatt (1971) showed that *M. spatulata* ( $2n = 12$ ) (subg. *Grandiflorae*) has about twice as much chromosome material as *M. ramosissima* (subg. *Moraea*) and *Diets*, both  $2n = 20$ . By extension, we infer a genome size in subg. *Grandiflorae* of about twice that for diploid species of other subgenera, excluding *Viesseuxia* sect. *Villosae*.

#### Karyotype morphology

Although not clear from early illustrations made using sections of root tips (e.g. Goldblatt 1971), the  $x$



= 10 karyotypes appear moderately bimodal under root tip squash methods (Goldblatt 1976a; Goldblatt & Takei 1997). The chromosome complements consist of three long acrocentric chromosome pairs and seven medium to short  $\pm$  acrocentric pairs about half the length of the long pairs, e.g. in *M. elisiae* (subg. *Visciramosae*), *M. anomala* (subg. *Monocephalae*) and even in *M. herrei* (Goldblatt 1976c as *Barnardiella spiralis*) and *M. namibensis* (subg. *Polyanthes*). Karyotypes in *Ferraria*, sister to *Moraea*, are comparable, as are those for *Dietes* (Goldblatt 1971, 1981a; De Vos 1979), sister to *Ferraria* + *Moraea* (Goldblatt et al. 2002; Schnitzler et al. 2011). Most species have small satellites on the distal end of one of the longest chromosome pairs but satellite position is variable and satellites are located in different positions in several species.

Each of the three subgenera in which  $x = 6$  is ancestral are characterized by somewhat different karyotypes, thus consistent with a hypothesis that the reduced base number evolved independently in each. In subg. *Grandiflorae* karyotypes are strongly conserved and are fairly symmetric, with all chromosomes acro- to subtelocentric. Size differences are minimal in all species counted (Goldblatt 1971) but the longest and fourth longest pairs are consistently acrocentric. Satellites are located on the short arm of a long telocentric chromosome pair (third longest pair of the complement) in most species counted.

Karyotypes in subg. *Homeria* are also conserved and symmetric in all species with  $x = 6$ . The complement comprises six nearly equal acrocentric pairs, with a small satellite located on the distal end of the short arm of one of the two longest pairs (Goldblatt 1971, 1980a). In the three species with lower numbers,  $2n = 10, 9$  and  $8$ , karyotypes are asymmetric and include one or more pairs of very long metacentric chromosomes  $\pm$  twice the length of the acrocentrics.

Subg. *Viesseuxia* exhibits some variation in its karyotypes, but in general the largest chromosome pair is metacentric or almost so and there are two additional, smaller metacentric or submetacentric pairs. The position of satellites is especially variable, but small satellites are located on the short arm of a long, acrocentric chromosome pair in the majority of species examined cytologically (*Moraea algoensis*, *M. amabilis*, *M. barnardii*, *M. caeca*, *M. calcicola*, *M. cuspidata*, *M. loubseri*, *M. marionae*, *M. tricuspidata*, *M. unguiculata*, *M. worcesterensis*). A notable exception is *M. tripetala*, in which a large satellite is present on the short arm of a nearly telocentric chromosome pair (Goldblatt & Manning 2012). This feature readily separates it from close allies, which have different karyotypes, most of them typical of the subgenus.

Other notably different karyotypes in subg. *Viesseuxia* include very large satellites on the short arm of an acrocentric chromosome pair in *Moraea insolens* and *M. lurida*, a closely allied species pair, and small satellites in the longest, metacentric pair in *M. belendenii*, *M. mutabilis*, *M. tubbaghensis* and *M. villosa*. Particularly unusual for the subgenus, the karyotype of the taxonomically isolated *M. thomasiae* has five acrocentric chromosome pairs, one submetacentric pair,

and unusually large satellites on the short arm of a long acrocentric pair, a feature reminiscent of the karyotype of *M. tripetala*. *M. fergusoniae*, the only species of the subgenus with multiple leaves (and referred in the past to subg. *Moraea*) has a karyotype comparable to that of *M. thomasiae* with large satellites on a long acrocentric chromosome pair, but the smallest chromosome pair is metacentric (Goldblatt 1971, 1976a and unpublished). Evidently chromosome rearrangement, often involving the position of the satellite, has been important in the evolution of the subgenus, and is sometimes a useful indicator of phylogenetic relationship among species. Karyotypes are, as far as known, consistent within a species but most (with the exception of *M. fergusoniae*, *M. tripetala* and *M. amabilis*) are known from only one or two counts, rendering this conclusion open to verification.

In subg. *Polyanthes*, karyotypes of sect. *Polyanthes* and *Pseudospicatae*, with  $x = 6$ , are comparable and differ mainly in the position of the satellites. The longest and one other pair are submetacentric and the remaining pairs are acrocentric. The karyotype of *M. polystachya* documented by Goldblatt (1976a) has a small satellite at the distal end of the long arm of the longest acrocentric pair, the same karyotype as in *M. venenata* (published as *M. polystachya* and not illustrated). Other species examined have small satellites on a small acrocentric pair. Satellite position is evidently variable, even with the same species (e.g. in *M. crispa* and *M. polyanthos*) and evidently without taxonomic significance (Goldblatt 1980a, 1986c). One of two populations of the Tanzanian *M. callista* examined is structurally heterozygous with one long and one short metacentric chromosome (Goldblatt & Takei 1997), the significance of which remains to be established.

In sect. *Hexaglottis* the ancestral karyotype consists of six nearly equal acrocentric pairs, with a small satellite present on the distal end of the short arm of one of the two longest pairs (Goldblatt 1987b). *Moraea lewisiae* subsp. *secunda* has a distinctive karyotype for the group, with the longest chromosome pair metacentric and with a small satellite located at the distal end of the shortest chromosome pair. As discussed in more detail below, in *M. virgata* ( $x = 6$ ), southwestern Cape populations of subsp. *virgata* have  $2n = 10$  and *M. virgata* subsp. *karooica* has  $2n = 14$ , thus both one subspecies is dysploid and the other has dysploid populations. The basic karyotype in the section recalls that in subg. *Homeria*, evidently the result of convergence.

The karyotype in sect. *Gynandris* is the most distinctive in subg. *Polyanthes*, consisting of one long metacentric pair, one small metacentric pair and four moderate-sized acrocentrics, one or sometimes two of which have large satellites on their short arms. The polyploid *M. monophylla* and *M. sisyrinchium* have the same karyotype with two sets of chromosome pairs otherwise matching the diploid karyotypes. Evidence is consistent with an independent origin of  $x = 6$  in sect. *Gynandris* and a shared origin of that base in sect. *Polyanthes* and sect. *Pseudospicatae*, but possibly not for sect. *Hexaglottis*.



## Dysploidy

There are six known dysploid species in *Moraea*: *M. indecora* and *M. papilionacea* (subg. *Moraea*), *M. variabilis* and *M. minima* (subg. *Galaxia*), and *M. demissa* and *M. flavescens* (subg. *Homeria*). Several more have euploid and dysploid populations. In addition, subg. *Galaxia* is itself dysploid, as is ser. *Eurystigma* of subg. *Galaxia*. Subgenera *Grandiflora*, *Vieusseuxia* and *Homeria*, all  $x = 12$ , are dysploid as are four of six sections of subg. *Polyanthes*. Dysploidy in populations of otherwise euploid species is associated with no visible morphological changes except in *M. virgata*. Here the taller, larger-flowered subsp. *karooica* has an extra pair of small chromosomes, thus  $2n = 14$  (vs.  $2n = 12$  in 5 populations of subsp. *virgata* and  $2n = 10$  in four more) and is sufficiently distinct in morphology to merit taxonomic separation. All but one of these examples clearly represents descending dysploidy.

Among the dysploid species two different patterns of chromosome rearrangement are evident. The first is exemplified by *M. indecora* ( $2n = 16$ ), which has two large metacentric pairs (plus one long acrocentric pair bearing a small satellite on the short arm and five short  $\pm$  acrocentric pairs) whereas its relatives with  $2n = 20$  have only acrocentric chromosomes. The reduction in base number is best explained by fusion of small chromosome pairs, the probable result of Robertsonian translocation (the product of unequal reciprocal translocation and loss of a pair of centromeres, *vide* Jones 1970). In *M. papilionacea*, which has populations with  $2n = 18$  and  $2n = 16$ , there are one or two pairs of large metacentric chromosomes respectively (Goldblatt 1971 and unpublished).

In subg. *Galaxia* both this and a second pattern, the absence of metacentric chromosomes in the dysploid derivatives, are evident. The subgenus has a basic karyotype with the derived  $2n = 18$  and consists of 9 pairs of acrocentric chromosomes. Base number in ser. *Eurystigma* is  $x = 8$ , again derived, and consisting only of acrocentric chromosome pairs. However, dysploid populations of *M. versicolor* with  $n = 7$  have a pair of large metacentric chromosomes. *M. variabilis* is also dysploid,  $n = 7$ , but the karyotype consists only of acrocentric pairs (Goldblatt 1979a).

In the most striking example of descending dysploidy, *Moraea fugax* displays a sequence of diploid chromosome numbers from the ancestral  $2n = 20$  to 10 (Goldblatt 1986b). In the blue- or white- or pink-flowered morph, karyotypes with  $n = 10$ , 9 and 8 have exclusively acrocentric chromosomes but the  $n = 7$  morphs have the largest pair metacentric and one  $n = 6$  morph has two large metacentric chromosome pairs. In the yellow-flowered morph of the species with  $n = 8$ , 7 and 5, the  $n = 8$  population has the largest pair metacentric, the  $n = 7$  population has two large metacentric pairs and the  $n = 5$  pair has the three largest pairs metacentric.

In these examples, the dysploid populations or taxa thus exhibit both patterns of karyotype change with about equal frequency.

## DISCUSSION

In *Moraea*, only narrowly endemic species can be confidently predicted to have a single chromosome number. In more widespread species, multiple counts for different populations across their ranges are needed to establish chromosome number. Of 166 species counted, no less than 14 species have diploid and polyploid populations and another seven have euploid and dysploid populations at the diploid level and one at the polyploid level (*M. inclinata*). Chromosome number and karyotype in *Moraea* are unusually variable compared to most other genera of Iridaceae in sub-Saharan Africa, which mostly display very conservative karyotypes. However, in *Lapeirousia* and *Romulea* (subfam. Crocoideae) at least, dysploidy and subsequent polyploidy have been involved in their evolution and speciation (Goldblatt & Takei 1993, 1997). Although many species of *Moraea* remain to be examined cytologically, uncounted species are mostly in the species-rich subg. *Grandiflorae* and subg. *Vieusseuxia*, both of which to date have exhibited no variation in chromosome base number and, in subg. *Vieusseuxia*, only moderate variation in karyotype.

## Polyploidy

Although believed to be a significant mode of speciation in many floras (Stebbins 1950, 1971; and see review by Soltis *et al.* 2010), polyploidy appears relatively unimportant in the rich geophytic flora of sub-Saharan Africa, and of particularly the Greater Cape flora. Just 11 of the 166 species of *Moraea* for which we have counts are exclusively polyploid, thus less than 7%, and 15 more (9%) have diploid and polyploid populations. Of the polyploid species, two are Eurasian, thus only 9 of 164 sub-Saharan (African) species of *Moraea* counted (5.5%), are exclusively polyploid. This is consistent with a low frequency of neopolyploidy in other sub-Saharan geophytic monocot families.

For example, in Hyacinthaceae, which are particularly well represented in southern Africa, available counts in subfam. Hyacinthoideae show that 16 of 101 counted species (16%) of *Eucomis* L'Herit, *Lachenalia* J.Jacq. ex Murray and *Massonia* Thunb. ex Hoult. are exclusively polyploid, and a further 18 (18%) have diploid and polyploid populations (Goldblatt *et al.* 2012). However, five genera, including *Eucomis*, have polyploid base numbers, and are thus evidently palaeopolyploid. In sub-Saharan members of subfam. Ornithogaloideae (Goldblatt & Manning 2011), only one of the 24 species of *Ornithogalum* L. and three of 23 species of *Albuca* L. subg. *Albuca* counted are exclusively polyploid. In subfamily Urgineoideae only one of 14 counted sub-Saharan species of *Drimia* Jacq. is exclusively polyploid (7%). In contrast, polyploidy is relatively frequent in Eurasian species of *Ornithogalum*, *Drimia* and most of the larger genera of Hyacinthoideae. Among southern African Amaryllidaceae and Colchicaceae, both smaller geophyte families, there are no recorded polyploid species.

In other Iridaceae, only five of 70 (7%) sub-Saharan species of *Gladiolus* L. sampled cytologically so far have polyploid populations whereas all 10 to 12 Eurasian species are exclusively polyploid (Goldblatt *et al.*

1993). Among other sub-Saharan genera of Iridaceae subfam. Crocoideae with at least 10 species the frequency of neopolyploidy ranges from 0% (*Babiana* Ker Gawl., *Crocoshia* Planch., *Freesia* Klatt, *Hesperantha* Ker Gawl., *Tritonia* Ker Gawl.), to 3–6% (*Romulea* Maratti, *Sparaxis* Ker Gawl., *Watsonia* Mill.) to 8–12% (*Geissorhiza* Ker Gawl., *Ixia* L.) based on current, moderate sampling (Goldblatt 1971, 1985b; Goldblatt & Takei 1997).

Dysploidy provides a means of reproductive isolation in populations in the same way as polyploidy; and thus appears to have played almost as much a role in evolution and, by inference, speciation in *Moraea* as has polyploidy. Five species and one subspecies are what may be called neodysploids (dysploid at and below species rank) vs. 11 neopolyploids. More important, four subgenera (*Galaxia*, *Grandiflorae*, *Homeria* and *Vieusseuxia*) are palaeodysploid, as are ser. *Eurystigma* of subg. *Galaxia* and also sections *Hexaglottis*, *Gynandiris*, *Polyanthes* and *Pseudospicatae* of subg. *Polyanthes*. Dysploidy appears to be largely unidirectional in *Moraea*, with all but one example of dysploidy most parsimoniously inferred as descending. There is just one instance of ascending dysploidy, in *M. virgata* subsp. *karooica*, in which the karyotype has one small additional chromosome pair in both of the two populations examined (of three currently known).

*Moraea* is therefore one of the relatively few genera of flowering plants in which polyploid changes in chromosome number and chromosome rearrangement leading to dysploidy have been established as important factors in its early diversification and subsequent more recent speciation. Considerations of the determinants of speciation need to take these phenomena into account as much as geography and ecological factors such as shifts in soil, habitat and climate preferences, and reproductive and pollination biology. Chromosome rearrangement and polyploidy have played important roles in the evolution of the genus as well as in recent speciation.

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# Exsiccatae in the bryophyte collection of the National Herbarium, Pretoria

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**Keywords:** Bryophyte collection, exsiccatae, exchange, Pretoria National Herbarium, South Africa

## ABSTRACT

Exsiccatae in the bryophyte collection of the National Herbarium in Pretoria (PRE) are catalogued for the first time. Most of the 66 series represented in PRE were issued in Europe, but the USA is the country where the largest number of exsiccatae originated. The exsiccatae span three centuries, with the earliest specimens issued in 1845 and the latest in 2009. This indicates the long-standing exchange of material and transfer of knowledge between herbaria in South Africa and countries of the northern Hemisphere. Many of the exsiccatae in PRE are incomplete and specimens were received as duplicates in exchange sets rather than exsiccatae. PRE houses a number of important African and southern hemisphere exsiccatae including two different sets of A. Rehm's *Musci Austro-Africani* (1875–1877) and *Musci Austro-Africani cont.*, and R. Ochrya's *Bryophyta Antarctica exsiccata*.

## INTRODUCTION

The Cryptogamic Herbarium of the South African National Biodiversity Institute (SANBI), which forms part of the National Herbarium in Pretoria (PRE) (acronyms according to Holmgren *et al.* 1990), consists of three separate collections: (1) the mosses, (2) liverworts and hornworts, and (3) lichens. The PRE bryophyte collection (mosses, liverworts and hornworts), as well as other bryophyte collections in southern Africa, were described by Magill (1980). The bryophyte collections of the Rhodes University Herbarium (RUH), Compton Herbarium (NBG, including SAM), KwaZulu-Natal Herbarium (NH, on permanent loan), and Stellenbosch Herbarium (STE) were since incorporated into PRE.

The PRE bryophyte collection consists of approximately 69 000 specimens, of which 35 500 are from southern Africa (the region south of the Limpopo and Kunene rivers) and recorded in SANBI's PRECIS database (Magill *et al.* 1983). The remainder of the collection comes from many parts of the world and consists mainly of duplicate specimens received as gifts and through an intermittent exchange programme with more than 20 overseas herbaria. A substantial number of exsiccatae specimens, distributed throughout the main collection, were received through the exchange programme.

*Exsiccatae* (plural form of *exsiccata*, from the Latin *exsiccatus* for 'dried up') are series of published, uniform, numbered sets of dried specimens with printed labels (Sayre 1969; Pfister 1985; Triebel *et al.* 2004). Exsiccatae usually have descriptive titles with an indication of the editor and the place and date of issue or publication. They are distributed in several identical sets of duplicate specimens, usually accompanied by printed booklets of labels or *schedae* (e.g. Figure 1A). According to Art. 30.4 of the *International Code of Botanical Nomenclature* (McNeill *et al.* 2006), printed matter accompanying exsiccatae are, from 1 January 1953, only

effectively published if it is also distributed independently of the exsiccatae. Exsiccatae were often distributed in units of 100 specimens, a century; each century generally constituted a volume in the series.

Stafléu (1972) provided a general historical account of exsiccatae, while Triebel *et al.* (2004) discussed the historical development, scope and function of cryptogam and fungus exsiccatae. Exsiccatae of African bryophytes were summarized by Ochrya & Pócs (1992). Of the  $\pm 1\ 100$  cryptogam and fungus exsiccatae issued up to 2003, about 500 contain bryophytes (Triebel *et al.* 2004).

Type specimens and exsiccatae are generally regarded as the most valuable collections in a herbarium. Magill (1980) compiled a catalogue of southern African moss type specimens in PRE. The aim of this paper is to document and determine the extent of exsiccatae in the PRE bryophyte collection. Hopefully this will point to exsiccatae as well as parts of exsiccatae that are sought after by researchers.

## MATERIALS AND METHODS

Data on exsiccatae in PRE were gathered from specimens and published *schedae* in the PRE bryophyte herbarium, the series *Cryptogamae Exsiccatae* by Sayre (1969, 1971, 1975), *IndExs—Indexes of Exsiccatae*, a web-accessible database of exsiccatae established by Triebel & Scholz (2001) and maintained by staff members of the Botanische Staatssammlung München (M), as well as other publications referred to in the text and in Table 1. Terminology follows that of Triebel *et al.* (2004).

Only exsiccatae in the strict sense of Sayre (1969, 1975) are listed; therefore series in PRE that do not meet all the requirements of a published exsiccata, e.g. *Herb. Ind. Or. Hook. fil. & Thompson* (Sayre 1975: 343) and *Sammlung deutscher Laubmoose, Lebermoose und Flechten, Vol. I. Laub- und Lebermoose* by D. Dietrich, published in Jena (Germany) in 1861, which was issued



TABLE 1.—Exsiccatae in the PRE bryophyte collection

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
American Hepaticae. Prepared by Carolyn Coventry Haynes	Printed	Decades 1–12	1–120, incomplete	1907–1913	Haynes, C.C.	Highlands, New Jersey, USA
Bryophyta Africana Selecta	Printed	Series I–VIII	1–200	1992–1993	Ochrya, R. & Pócs, T.	W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland and Department of Botany, Eszterházy Károly Teachers Training College, Eger, Hungary
Bryophyta Antarctica exsiccata	Title, editor, place of issue and name printed, rest typewritten		1–200	1982	Ochrya, R.	W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland
Bryophyta Arduennae exsiccata	Fr. Verdoorn. Bryophyta Arduennae Exsiccata	Decades 1, 2 3	1–20 21–30	1927 1928	Verdoorn, F.	Utrecht, The Netherlands
Bryophyta Danica exsiccata	Printed	Parts II, III	93–283	1952, 1953	Holmen, K.A.	Botanical Museum, University of Copenhagen, Denmark
Bryophyta exsiccata Terrae-Novae et Labradorica	Typewritten	Fascicle 3	51–75, incomplete	1979	Brassard, G.R.	Memorial University of Newfoundland, St. John's, Canada
Bryophyta in itinere polari Norvegicum secundo collecta	Title, headings and collector printed on brown paper, rest filled in by hand		?, scattered numbers	Collected in 1898 & 1899	Simmons, H.G.?	Sweden
(Not listed by IndExs)						
Bryophyta Neotropica exsiccata	Printed	Fascicles VII, VIII	301–400	1996, 1998	Gradstein, S.R.	The University of Göttingen Herbarium (GOET), Germany
Bryophyta selecta exsiccata	H. Inoue: Bryophyta Selecta Exsiccata	Fascicle 1–?	1–?1 000, many missing	1970–?	Inoue, H.	National Science Museum, Tokyo (TNS), Japan
Bryophyta Typorum Exsiccata	Printed	Decades 1, 2	1–20	1981	Buck, W.R.	The New York Botanical Garden, USA
Bryotheca Bohemica. Laub- und Lebermoose aus Böhmen in getrockneten Exemplaren	Bauer, Bryotheca Bohemica, No.	Centuries 1–4	1–400, incomplete	1898–1904	Bauer, E.	Smitehov near Prague, Czech Republic
Bryotheca Brasilensis, herausgegeben von Dr. C. H. Brotherus in Helsingfors, bestimmt von Carl Müller, C. H. Brotherus und C. Warnstorf	Printed	Century 3	201–240, scattered numbers	1899	Brotherus, V.F.	Helsinki, Finland; duplicates received on exchange from H
Bryotheca Europaea. Die Laubmoose Europa's unter Mitwirkung mehrerer Freunde der Botanik gesammelt und herausgegeben von Dr. L. Rabenhorst	Rabenhorst, Bryotheca europaea	Fascicles 1–27	1–1 350 incomplete, many missing	1858–1876	Rabenhorst, G.L.	Dresden, Germany
	Printed as well as handwritten labels	Revised Sphagna	?, scattered numbers	1888?		



TABLE 1.—Exsiccatae in the PRE bryophyte collection (continue)

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
Bryotheca Fennica, edidit V. F. Brotherus	V. F. Brotherus. Bryotheca Fennica Printed on brownish paper	Fascicles 1–4	1–400, incomplete, many missing	1910–1916	Brotherus, V.F.	Helsinki, Finland
Campylopodetes Brasiliae exsiccatae	Printed	Fascicle 1	1–32	1978	Frahm, J.-P.	University of Duisburg, Germany
Campylopodetes exsiccatae	Printed	Fascicles I–III	1–75	1980–1983	Frahm, J.-P.	University of Duisburg, Germany
Canadian Hepaticae, collected and distributed by John Macoun, named by W. H. Pearson	Canadian Hepaticae Title, locality and collector printed, rest handwritten, some without numbers		1–116, scattered numbers	1891	Macoun, J.	Ottawa, Canada
Canadian Musci	Canadian Musci. Prepared by J. Macoun Printed		1–670, but only No. 575 seen, changed to 23a	1889–1893 (1908?)	Macoun, J.	Ottawa, Canada
Flora exsiccata Austro-Hungarica, a museo botanico universitatis vindobonensis edita	Flora Exsiccata Austro-Hungarica Printed	Fascicles 1–10, Centuries 1–20 Fascicles 15–16, Centuries 29–32	1–2 000, incomplete, many missing 2 801–3 600, incomplete, many missing	1881–1888 1898–1902	Kerner von Marilaun, A. Fritsch, K.	Vienna, Austria
Flora Germanica exsiccata. Serie II. Cryptogamia	Printed, without title	Century 1 2 3	1–100 101–200 201–300 Scattered numbers	1860 1843 1849	Breutel, J.C.	Leipzig, Germany
Flora Germanica exsiccata. Serie II. Cryptogamia. Centuria I. 2te Auflage	Breutel Hepat. exsicc. Printed		85–92	1860	Breutel, J.C.	Leipzig, Germany
Flora Graeca exsiccata			1–7800, at least one bryophyte (138) in PRE	1853–1862	Orphanides, T.G.	Athens, Greece
Flora Hungarica exsiccata a sectione botanica musei nationalis Hungarici edita	Sectio Botanica Musei Nationalis Hungarici. Budapest. Flora Hungarica exsiccata Printed	Centuries 1–X	1–1 000, incomplete, many missing	1912–1932	Anonymous	Sectio Botanica Musei Nationalis Hungarici, Budapest, Hungary
Fontinalaceae exsiccatae	Printed	Fascicles 1–4 6	1–135 159–174	1986–1994 2008	Allen, B.H.	Missouri Botanical Garden, St. Louis, USA
Grimmiae et Andreaeae exsiccatae	Printed, without title		1–50, scattered numbers	1861	Zetterstedt, J.E.	Uppsala, Sweden

TABLE 1.—Exsiccatae in the PRE bryophyte collection (continue)

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
Hepaticae Boreali-Americanae exsiccatae; or specimens of North American liverworts. Arranged by Coe Finch Austin	Printed on pale blue paper, without title		1–150, incomplete	1873	Austin, C.F.	Closter, New Jersey, USA
Hepaticae Britannicae exsiccatae	Printed on pale brown paper, without title	Fascicles 1–101	1–215	1878–1883	Carrington, B. & Pearson, W.H.	Manchester, UK
Hepaticae exsiccatae S.O. Lindbergii	Printed	Fascicle I III, IV	1–230 335–568	1993 1996, 1997	Piippo, S.	Botanical Museum, University of Helsinki, Finland
Hepaticae Japonicae exsiccatae	Hepaticae Japonicae	Series I, 2	1–100, incomplete	1946, 1947	Hattori, S.	The Hattori Foundation for Botanical Research, Obi, Japan
Hepaticae macroregioni meridionali Poloniae exsiccata. Liverworts of Southern Macrotregion of Poland	Printed					
	Hepaticae Macroregioni Meridionali Poloniae Exsiccata. Fasc.	Fascicles I–VIII XVI, XVII	1–120 226–325	1982–1997 2002, 2004	Jedrzejko, K., Zamowice, J., Klania, H. & Siebel, A., in different combinations	Herbarium of the Department of Pharmaceutical Botany (SOSN), Silesian Medical School in Katowice, Sosnowice, Poland
	Fasc. I and 2 typewritten, rest printed					
Hepaticae selecti et critiei, editit Fr. Verdoorn	Hepaticae Selectae et Criticae	Series I–XI	1–550	1930–1939	Verdoorn, F.	Utrecht, The Netherlands
Herbarium normale. Herbar des plantes nouvelles peu connues et rares d'Europe principalement de France et d'Allemagne. Cryptogamie	Printed					
	F. Schultz et F. Winter, herbarium normale. Cryptogamia. Cent.1		1–100, scattered numbers	1872	Schultz, F. & Winter, F.	Wissenbourg, France
Herbarium normale. Herbar des plantes nouvelles peu connues et rares d'Europe principalement de France et d'Allemagne publié par F. Schultz	Printed on brown paper with black frame					
	F. Schultz, herbarium normale. Cent.	Centuries 1, 2 7–12	1–200 601–1 200 Incomplete	1856 1864–1869	Schultz, F.W.	Wissenbourg, France
Herbarium normale. Herbar des plantes nouvelles peu connues et rares d'Europe principalement de France et d'Allemagne publié par F. Schultz. Nouvelle. série, publié par Dr. K. Keck et Dr. J. Scriba	Printed on brown paper with black frame					
	F. Schultz, herbarium normale, nov. ser. Cent.	Century 4	301–400, scattered numbers	1879	Keck, K.[C.] & Scriba, J.K.	Aistersheim, Austria

TABLE 1.—Exsiccatae in the PRE bryophyte collection (continue)

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
Herbarium normale. Nov. ser. Herbier des plantes nouvelles peu connues et rares d'Europe principalement de France et d' Allemagne publié par F. Schultz	F. Schultz, herbarium normale, nov. ser. Cent. Printed on brown paper with black frame	Century 1	1–100, scattered numbers	1874	Schultz, F.W.	Wissembourg, France
Iter Faeroense 1895	H. G. Simmons, Iter faeroense 1895		?, scattered numbers	± 1896	Simmons, H.G.	Sweden
	Title, determiner and collector printed, rest handwritten					
Kryptogamae exsiccatae editae a Museo Palatino Vindobonensi	Kryptogamae exsiccatae Printed	Century 1  7	1–100, scattered numbers  601–700, scattered numbers	1894  1901	Anonymous  Zahlbruckner, A.	Museum Hist. Natur. Vindobonensis, Vienna, Austria
L. Rabenhorstii Bryotheca Europaea et Extraeuropaea. Die Laubmoose Europa's (und anderer Erdteile) unter Mitwirkung mehrerer Freunde der Botanik gesammelt und herausgegeben von Dr. G. Winter	Rabenhorst – Winter, Bryotheca europaea Printed	Fascicle 28	1 351–1 400, scattered numbers	1884	Winter, G.	Dresden, Germany
Maine Mosses	Printed on yellowish paper	Fascicles 1–8	1–386, scattered numbers	1999–2007	Allen, B.H. & Pursell, R.A.	The Missouri Botanical Garden, St. Louis, USA
Mosses of Colorado. Distributed by J. M. Holzinger; collected by Carl F. Baker 1896	Mosses of Colorado Printed on brownish paper with no. name and other info handwritten		1–50, incomplete	After 1896	Holzinger, J.M.	State Teachers College, Winona, Minnesota, USA
Mosses of Minnesota. Distributed by J. M. Holzinger	Mosses of Minnesota Title and distributor printed, rest filled in by hand, without numbers		?, scattered numbers	From 1902?	Holzinger, J.M.	State Teachers College, Winona, Minnesota, USA
Mosses of the Hawaiian Islands	Printed		1–20, scattered numbers	1907?	Small, J.K.	Originally New York, USA, but received on exchange from NY
Mosses of the Southern United States, distributed from the Herbarium of Columbia College [University] by John K. Small	Mosses of the Southern United States Printed		1–51, incomplete	1897	Small, J.K.	Originally Herbarium of Columbia College (University), New York, USA., but received on exchange from MU
Musci Acrocarpi Boreali-Americani. Distributed by John M. Holzinger	Musci Acrocarpi Boreali-Americani Printed on brownish paper	Fascicles 1, 3	1–25, 51–75, incomplete	1904	Holzinger, J.M.	Originally Winona, Minnesota, USA, but received on exchange from MU



TABLE 1.—Exsiccatae in the PRE bryophyte collection (continue)

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
Musei Appalaehiani. Tickets of specimens of mosses collected mostly in the eastern part of North America by C.F. Austin	Printed on pale blue paper, without title		1–450, incomplete	1870	Austin, C.F.	Closter, New Jersey, USA
Musei Australasiae exsiccati	Printed	Faseicles 1–18	1–600	1992–2000	Streimann, H.	Cryptogamic Herbarium, Australian National Botanic Gardens (CBG), and later Centre for Plant Biodiversity Research (CANB), Canberra, Australia
Musei Austro-Africae (1875–77) (Two different sets in PRE)	Original labels in NH with printed title, rest in Rehmann's handwriting  Sim labels in his handwriting, without title		1–424, incomplete	1878–1879	Rehmann, A	Kraków, Poland
Musei Austro-Africae cont. (Two different sets in PRE)	Original labels in NH handwritten, with title  Sim labels in his handwriting, without title		425–680, incomplete	1886	Rehmann, A	? Lviv, Ukraine
Musei Britanniei	W. Wilson: Musei Britanniei  Typewritten NY label		1–443, incomplete, many missing	After 1855	Wilson, W.	Originally Warrington, UK, but received on exchange from The New York Botanical Garden, USA
Musei et Hepaticae Italiae Sup. a F. A. Ariaria coll.	Title and major locality printed, rest handwritten		Largely unnumbered, few	1898	Artaria, F.A.	? Milan, Italy
Musei Europaei exsiccati. Die Laubmoose Europas unter Mitwirkung namhafter Bryologen und Floristen	E. Bauer, Musei europaei exsiccati  Some printed, others typewritten	Series 18 22–30	851–900 1 051–1 500, incomplete	1912 1915–1922	Bauer, E.	Prague, Czech Republic
Musei Europaei exsiccati et Americani exsiccati	Bauer, Musei europ. et amer. exsiccati	Series 44	2 151–2 200, scattered numbers	1932	Bauer, E.	Prague, Czech Republic
Musei Galliae, herbier des mousses de France, Belgique, etc.	Printed  Husnot, Musei Galliae  Most printed, others handwritten	Faseicles 1–19	1–959, incomplete, many missing	1870–1907	Husnot, P.T.	Cahan, France
Musei Japoniei exsiccati	Musei Japoniei	Series 1	1–50	1947	Anonymous	The Hattori Botanical Laboratory, Obi, Japan
	Printed	2	51–100	1948	Hattori, S.	

TABLE 1.—Exsiccatae in the PRE bryophyte collection (continue)

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
Musci macroregioni meridionali Poloniae exsiccati: Mosses of Southern Macregion of Poland	Musci Macroregioni Meridionali Poloniae Exsiccati Fasc.	Fascicles I–XII XXXI–XLII XLIV	1–350 801–1 400 1 451–1 500	1982–1997 2002–2004 2008	Jedrzejsko, K., Klama, H., Stebel, A. & Żarnowiec, J., in different combinations	Herbarium of the Department of Pharmaceutical Botany (SOSN), Medical University of Silesia in Katowice, Sosnowiec, Poland
Musci Madurenses Indiae meridionalis exsiccati, named by Jules Cardot (PRE specimens probably from a later set - see Sayre 1971: 201)	Fascicles 1–3 labels typewritten, rest printed Original label, if present, typed, with number and name only NY label typewritten, with title 'Mosses of Southern India', locality, and note 'Residue of Musci Madurenses Indiae Meridionalis Exsiccati'		1–2, scattered numbers	Later than 1929	Foreau, G.	Originally Madura, India, but 'residue' distributed by The New York Botanical Garden (NY), USA
Musci Mexicani	C. G. Pringle, Plantae Mexicanae Printed, or title printed and rest typewritten		1–2, Scattered numbers	1896–after 1908	Pringle, C.G.	USA
Musci selecti et critici, edidit Fr. Verdoorn	Musci Selecti et Critici Printed	Series I–VII	1–350, incomplete numbers	1934–1940	Verdoorn, F.	Utrecht, The Netherlands
North American Musci perfecti; issued by A.J. Grout Ph. D.	North American Musci Perfecti Printed on brownish paper		1–475, scattered numbers	1925–1945	Grout, A.J.	Originally Newfane, Vermont, USA, but received on exchange from MU
Orthotrichaceae Boreali-Americanae exsiccatae	Printed	Fascicles I–III	1–30	1980–1981	Vitt, D.H.	University of Alberta, Edmonton, Canada
Plantae Graecenses, Bryophyta	Plantae Graecenses		1–2, scattered numbers	After 1908	Anonymous	Institut für Botanik, Graz, Austria
Plantae in Itineribus Suecorum Polari-bus collectae/Insulae Spitsbergenses	Plantae in itineribus Suecorum polari-bus collectae Title, main locality and collector printed, rest handwritten on brown paper		1–199, scattered numbers	1874	Berggren, S.	Lund, Sweden
Schweizerische Kryptogamen. Unter Mitwirkung mehrerer Botaniker. Gesammelt und herausgegeben von Dr. B. Wartmann und B. Schenk	Wartmann und Schenk, Schweizerische Kryptogamen Printed	Century 6, Fasc. 11 & 12 Century 7, Fasc. 13 & 14	501–600, scattered numbers 601–700, scattered numbers	1866 1869	Wartmann, F.B. & Schenk, B.	St. Gallen, Switzerland

TABLE 1.—Exsiccatae in the PRE bryophyte collection (continue)

Full title according to IndExs	Labels in PRE (title and notes)	Parts in PRE	Numbers issued, present in PRE	Date of publication	Editor or distributor	Institution, place and country of publication
Société Dauphinoise	Société dauphinoise, 18...		1-?, scattered numbers	1879-? 1888	Anonymous	Société Dauphinoise pour l'échange des plantes, France
	Printed					
[South America. 1895-1897]	Printed, without titles		1-877?, scattered numbers	After 1897	Dusén, P.K.H.	Sweden?
Sphagnaceae Briamiaceae exsiccatae, edidit R. Braithwaite	Handwritten, without title, with black frame		1-53	1877	Braithwaite, R.	London, UK
	Numbers and names correspond to those of Wheldon (1919)					



in book form with the specimens mounted on the pages next to printed names, but without numbers and localities, are excluded.

In Table 1, the bryophyte exsiccatae in PRE are listed alphabetically by full title according to IndExs. Exsiccatae in IndExs, which obviously belong to the same series, e.g. *Musci Japonici exsiccati Det. A. Noguchi* (Ser. 1, 1–50) and *Musci Japonici exsiccati det. Akira Noguchi* (Ser. 2, 51–100), were combined. The second column contains notes on the labels in PRE, e.g. the title (if different from the full title), printing and colour. This is followed by the parts present in PRE and the numbers issued in each, with an indication of the numbers present in PRE. The remaining columns contain the date, institution, place and country of editing, publication or distribution, as well as the name of the editor or distributor. The analysis of exsiccatae in the bryophyte collection is based on data in Table 1.

## RESULTS AND DISCUSSION

The PRE bryophyte collection houses 66 exsiccatae (Table 1), which represent 6% of all cryptogam and fungus exsiccatae issued up to 2003 (Triebel *et al.* 2004) and 13% of cryptogam exsiccatae that contain bryophytes.

The majority of exsiccatae in PRE (34) were first issued in the 19th century, almost as many (32) in the 20th century, and none in the 21st century. The oldest exsiccatae specimens in PRE are from Century 2 of *Flora Germanica exsiccata. Serie II. Cryptogamia*, edited by J.C. Breutel and issued in Leipzig, Germany in 1843 (Figure 1B). The most recent specimens in PRE belong to Fascicle XXX of *Bryophyta selecta exsiccata*, edited by H. Inoue and issued in 2009 by the National Science Museum (TNS), Tokyo, Japan (Figure 1C). This indicates long-standing co-operation and exchange of scientific knowledge between herbaria in South Africa and countries of the northern Hemisphere.

Although exsiccatae usually have printed labels (see Figure 1B, C, G, H), there are series in PRE with handwritten labels, e.g. *Sphagnaceae Britannicae exsiccatae*, edited by R. Braithwaite, which was issued in 1877 (Figure 1D), typewritten labels, e.g. Fascicles 1–3 of *Musci macroregioni meridionali Poloniae exsiccati. Mosses of southern macro-region of Poland*, issued by SOSN from 1982 to 1984, and a combination of the above, e.g. S. Berggren's *Plantae in Itineribus Suecorum Polaribus collectae/Insulae Spitsbergenses* from 1874, with title, main locality and collector printed and rest handwritten (Figure 1E), and R. Ochrya's *Bryophyta Antarctica exsiccata*, issued in 1982, with the title, editor, place of issue and name printed, and the rest typewritten (Figure 1F). Several of the 19th century series have printed labels without titles, which make them difficult to recognize, e.g. C.F. Austin's *Musci Appalachiani*, as well as *Hepaticae Boreali-Americanae exsiccatae* (Figure 1G) issued in 1870 and 1873 respectively, and Carrington & Pearson's *Hepaticae Britannicae exsiccatae* of which Fascicles 1–3, issued from 1878 to 1883, are represented in PRE.

Most exsiccatae in PRE were issued in Europe (44), followed by North America (18), Asia (3) and Australasia (1). However, the United States of America (14) is the country where most exsiccatae in PRE originated from, followed by Germany with seven, Poland with six, and France and Sweden with five exsiccatae each.

The majority of bryophyte exsiccatae in PRE are incomplete (Table 1), some only represented by single specimens, which indicates that they were distributed as duplicates in exchange sets rather than exsiccatae, e.g. *North American Musci perfecti; issued by A. J. Grout Ph.D.* in Newfane, Vermont from 1925 to 1940, of which there are only a few specimens in PRE, received on exchange from the W.S. Turrell Herbarium, Miami University (MU) in 1990 (Figure 1H). Another example is *Musci Britannici*, edited by W. Wilson and originally issued in Warrington, UK after 1855, but the few scattered numbers in PRE were only received in the latter part of the 20th century through exchange with The New York Botanical Garden (NY).

PRE houses two different sets of Antoni Rehmman's *Musci Austro-Africani* (1875–77) and *Musci Austro-Africani cont.*, regarded as the most important African exsiccatae (Ochrya & Pócs 1992). One set was compiled by T.R. Sim and housed in his private herbarium, now in PRE (Magill 1980; Codd & Gunn 1982), while the other is on permanent loan from the KwaZulu-Natal Herbarium (NH). The sets contain several southern African type specimens but are incomplete (Dixon & Gepp 1923; Magill 1980; Codd & Gunn 1982; Glen & Germishuizen 2010).

Another important African exsiccata in PRE, the only to cover the whole of sub-Saharan Africa, is *Bryophyta Africana Selecta*, edited by Ryszard Ochrya and Tamás Pócs and issued jointly by the W. Szafer Institute of Botany in Kraków, Poland, and the Eszterházy Károly Teachers Training College, Eger, Hungary in 1992 and 1993. Frans Verdoorn's *Hepaticae selecti et critici*, as well as *Musci selecti et critici*, issued in the 1930's, contain bryophytes from several continents, including Africa.

PRE also contains important bryophyte exsiccatae from other parts of the southern hemisphere, e.g. *Bryophyta Antarctica exsiccata*, edited by Ryszard Ochrya and distributed by the University of Alberta, Edmonton, Canada in 1982 (Figure 1F), which is the first and only exsiccata of Antarctic bryophytes. The Australian series *Musci Australasiae exsiccatae*, edited by H. Streiman (Figure 1A), is one of the largest exsiccata in PRE with 600 specimens.

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## Notes on African plants

VARIOUS AUTHORS

### COLCHICACEAE

#### FIRST RECORD OF *GLORIOSA SESSILIFLORA* IN ANGOLA

##### INTRODUCTION

The genus *Gloriosa* L. was proposed by Linnaeus in 1737 and validated in 1753 (Linnaeus 1753). The type species for the genus is *G. superba* L., described from a specimen collected in southwest India (Malabar, present-day Kerala and part of Tamil Nadu). During the next  $\pm$  260 years, a further 40 species of *Gloriosa* were described (IPNI 2012), although the majority were subsequently reduced to synonymy. The most recently described species of *Gloriosa* is *G. sessiliflora* Nordal & Bingham (Nordal & Bingham 1998), a paper where the generic delimitation between *Gloriosa* and *Littonia* Hook. was first questioned. The connivent tepals of *G. sessiliflora* are similar to those of *Littonia*, although the colour, shape and undulation of the tepals strongly resemble those of some forms of *G. superba* (Nordal & Bingham 1998). The slightly bent style of *G. sessiliflora* also appears to be an intermediate trait.

The genus *Littonia* (Hooker 1853) differs from *Gloriosa* in its straight, not bent style and connivent, not reflexed tepals (Nordal & Bingham 1998), but there are many similarities between the two genera. Both have tuberous corms (Buxbaum 1937; Dyer 1976; Thulin 1995; Demissew 1997; Nordenstam 1998), their leaves frequently develop tendril-like tips (Queva 1899; Dyer 1976; Thulin 1995; Demissew 1997; Nordenstam 1998) and colchicine occurs in both (Hegnauer 1963; Wildman & Pursey 1968; Raffauf 1970; Vinnersten & Larsson 2010). Queva (1899) also noted that crystals of calcium oxalate were lacking in both *Gloriosa* and *Littonia*. The pistils of *Gloriosa* and *Littonia* are generally tricarpellate and alike (Sterling 1975). Because of such a series of resemblances, most investigators have been inclined to treat these genera as being closely related and have placed them in the same tribe (e.g. Krause 1930; Hutchinson 1934, 1959; Buxbaum 1936; Nordenstam 1982, 1998). Recent molecular phylogenetic studies on family Colchicaceae using three non-coding sequences from cpDNA retrieved a well-supported clade (100% jackknife support) in which *Littonia* species were nested among *Gloriosa* species (Vinnersten & Reeves 2003). Consequently, the genus *Gloriosa* has been expanded by including *Littonia* (Vinnersten & Manning 2007), rendering it monophyletic. The genus *Gloriosa* (including *Littonia*) is now classified as a member of the tribe Colchiceae (Vinnersten & Manning 2007).

This paper reports on the presence of *G. sessiliflora* in the Bié Province, central Angola. *Gloriosa sessiliflora* was described as endemic to Western Zambia (Nordal & Bingham 1998). The second known set of specimens

(Bingham 12717) were collected in 2003 in Lealui, in the vicinity of the type locality (Figure 1). During a taxonomic revision of the genus *Gloriosa* (Maroyi 2012), which started with examination of material in the National Herbarium of Zimbabwe (SRGH), it became clear that among material referred to *G. superba* L., was material matching the type of *G. sessiliflora* (Figure 2). Here I present an expanded description and distribution notes for *G. sessiliflora* and a photograph of the specimen collected in the Bié Province, central Angola.



Figure 1.—Distribution of *Gloriosa sessiliflora* based on georeferenced herbarium specimens.

##### TAXONOMY

***Gloriosa sessiliflora* Nordal & Bingham**, in Kew Bulletin 53: 479–482 (1998). TYPE: Zambia, Western Province, Mongu District, Bulobi floodplain,  $\pm$  2 km W of Lealui, 1 000 m, 9 Dec. 1995, Bingham & Luwika 10752 (K, holo.; MRSC, O, WAG!, iso.).

Perennial herb, corm tuberous, 2-pronged, L or V-shaped, covered with brown tunics, 50 mm long, 10–20 mm in diameter; roots fibrous. Stem erect, up to 1 000 mm tall, simple at flowering but later branching from below inflorescence, with numerous whorled leaves in upper two-thirds. Leaves sessile, entire, base sheathing stem with tubular sheath protracted or not protracted into leaf blade, blade lanceolate with cirrhose apex with prominent midrib, 70–130  $\times$  15–25 mm wide. Flowers suberect to slightly spreading, sessile, 2–8 per stem, solitary or paired in leaf axils near stem apex, funnel-shaped, tepals connate at base into short tube up to 4 mm long, glabrous, narrowly ovate, slightly undu-

late, 35–40 × 10–15 mm long, with prominent midrib, yellowish orange near base but reddish distally, nectariferous, obscurely saccate and pouched at base often with white hairs. *Stamen* filaments filiform, 16–31 mm long, yellowish, anthers 6 mm long, orange, versatile, dehiscence latrorse. *Ovary* oblong, 5–9 × 2–4 mm wide;

style slightly bent, suberect, 23–26 mm long, stigma 3-branched, branches 3 mm long. *Fruits and seeds* not seen.

*Diagnosis:* *G. sessiliflora* is distinguished from all other *Gloriosa* species by the sessile, suberect or slightly



Figure 2.— *Gloriosa sessiliflora*, Mendes dos Santos 1968 (SRGH). Photograph: L.J.G. van der Maesen.

spreading flowers, all other species having pendulous flowers on long pedicels.

**Distribution and ecology:** *Gloriosa sessiliflora* is now known from three collections, extending its western distribution limit in Bulozzi floodplain, Zambia to the Bié Province, central Angola (Figure 1). In western Zambia, *G. sessiliflora* grows in open woodland, about 1 000 m altitude. It has been recorded in *Syzygium* forest, flood plain termite mounds, and sand banks with riverine forest in Zambia. In Angola, it has been recorded in sandy soils. Mature flowers have been collected between October and December.

**IUCN conservation status:** IUCN conservation status of *G. sessiliflora* was assessed using herbarium specimen data. According to Rivers *et al.* (2011) and Willis *et al.* (2003), herbarium data can be used to determine IUCN categories of threat using criterion B (geographic range) and the number of locations as criterion D2 (small or restricted populations). According to Schatz (2000), herbarium specimens and their associated locality information must be accepted as sufficient for performing provisional IUCN conservation assessment on poorly known species. To qualify as threatened, a species must be assessed as CR, EN or VU (Willis *et al.* 2003). *G. sessiliflora* is represented by less than five accessions from both Angola and Zambia, mainly from unprotected areas. The lack of collections of *G. sessiliflora* in Angola since the first collection in the Bié Province in 1965 justifies the inclusion of the species in the IUCN Red List of threatened species in Zambia. It is probable that because of severe urban transformations in the Bié Province, the species no longer exists there. Therefore, the vulnerable (VU D2) status is recommended for the species. Previously, the species was categorized as vulnerable, VU D2 (Bingham & Smith 2002), mainly because it was only known from the type locality, characterized by very small and restricted population. The taxon might be transferred to a lower category if more populations are found.

### Specimens examined

ANGOLA.—(no grid): Bié Province, 6 Oct. 1965 (fl.), Meudes dos Santos 1968 (SRGH).

ZAMBIA.—(no grid): Western Province, Mongu District, Bulozzi floodplain, Lealui, 1 022 m, 1 Dec. 2003. Bingham 12717 (K).

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## POACEAE

TAXONOMIC SIGNIFICANCE OF EPIDERMAL STRUCTURE IN SOUTHERN AFRICAN MEMBERS OF *HELICTOTRICHON*

## INTRODUCTION

*Helictotrichon* Besser ex Schult. & Schult.f. (excluding *Avenula* (Dumort.) Dumort. and *Amphibromus* Nees) is a genus of temperate  $C_3$  grasses with about 40 species (Gibbs Russell *et al.* 1990; Mabberley 2008). The genus is most diverse in the temperate regions of the northern hemisphere, especially in Europe, from where it extends southwards along the African mountains (Afri-montane Region). This paper deals only with those species occurring in southern Africa, a secondary centre of diversity for the genus.

In a taxonomic revision based mainly on macromorphology, Schweickerdt (1937) recognized 12 species of *Helictotrichon* in southern Africa. A new taxonomic revision of the group (Mashau *in progress*), which also considered evidence from leaf anatomy, applied to all these species as well as two newly described ones (Mashau *et al.* 2010), thus bringing the total number of species on the subcontinent to 14. The anatomical attributes of the leaf epidermis of these species were studied for the first time and proved to be particularly useful for distinguishing among species. The purpose of the present paper is to report on the taxonomic significance of leaf epidermal characters in the southern African members of *Helictotrichon*.

*Helictotrichon quinquesetum* (Steud.) Schweick. is only known from two collections from the Cape Peninsula, both dating from the 19th century. The species is currently considered critically rare and is probably extinct (Helme & Raimondo 2010). Only fragments of the inflorescence from the type, *Ecklon 929* (removed from the holotype in OXF and isotype in K), are available at the National Herbarium (PRE). The original collections are also very poor and have hardly any leaves (seen on Aluka website). Hence, due to the limited material available, this species was not studied anatomically.

## MATERIALS AND METHODS

The epidermal structures of 13 *Helictotrichon* species were studied (see Table 1 for a list of species and voucher specimens). *H. quinquesetum*, a very rare species, was not studied (see above).

Portions of dried leaf blades were cut from herbarium specimens, transferred to test tubes containing distilled water and heated in a water bath at 50°C for about 24 hours. After allowing cooling for about 12 hours, the rehydrated leaves were fixed in formalin-acetic-acid-alcohol [FAA] (Johansen 1940) for at least 48 hours. Before further processing, the pieces of leaf blade were thoroughly washed in water to remove all traces of the fixative.

To obtain the epidermal peels, leaf blades were transversely cut into pieces of about 10 mm long, and

TABLE 1.—List of species and specimens examined

Species	Specimens examined
<i>H. barbatum</i> (Nees) Schweick.	<i>Acocks 18632</i>
<i>H. capense</i> Schweick.	<i>Story 3803; Tyson 20564</i>
<i>H. dodii</i> (Stapf) Schweick.	<i>Pole-Evans 499, 518</i>
<i>H. galpinii</i> Schweick.	<i>Ellis 1389; Hilliard &amp; Burt 16478</i>
<i>H. hirtulum</i> (Steud.) Schweick.	<i>Smook 5859; Spies 1695A</i>
<i>H. leoninum</i> (Steud.) Schweick.	<i>Ellis 225; Cleghorn 3130</i>
<i>H. longifolium</i> (Nees) Schweick.	<i>Smook 1184; Davidse 6962</i>
<i>H. longum</i> (Stapf) Schweick.	<i>Acocks 20691; Ellis 5432</i>
<i>H. namaquense</i> Schweick.	<i>Ellis 5997</i>
<i>H. natalense</i> (Stapf) Schweick.	<i>De Wet 1722; Rennie 1534</i>
<i>H. rogerellii</i> Mashau, L.Fish & A.E.van Wyk	<i>Ellis 4663</i>
<i>H. roggeveldense</i> Mashau, L.Fish & A.E.van Wyk	<i>Acocks 17178; Ellis 5117</i>
<i>H. turgidulum</i> (Stapf) Schweick.	<i>Smook 5888; Spies 3953</i>

one margin removed by cutting it off. The pieces were placed in stopper glass tubes, covered with Jeffrey's solution [equal volumes of 10% aqueous chromic acid ( $CrO_3$ ) and 10% nitric acid ( $HNO_3$ )] and left at room temperature for about 24 hours until the unwanted tissue between the upper and lower leaf epidermis had dissociated and was easily freed from the epidermis (Kiger 1971). The sufficiently macerated pieces of leaves were thoroughly washed in water and then stained with 1% safranin in 50% ethanol for about 30 minutes to 1 hour. The stained material was then dehydrated in a graded ethanol series: 50% ethanol; 70% ethanol; 94% ethanol; 100% ethanol followed by 50:50 ethanol and xylol; and finally 100% xylol (10 minutes in each solution). The leaf segments were finally opened like a book (abaxial and adaxial surfaces parted) and any remaining mesophyll removed and mounted in entellan (Product 7961, E. Merck, Darmstadt) under cover slips on microscope slides. The descriptive terminology for the leaf epidermal anatomy follows Ellis (1979).

## RESULTS AND DISCUSSION

The epidermis of the *Helictotrichon* leaf blade exhibits taxonomically significant variation in the structure and shape of the silica bodies, costal cells, intercostal short cells, stomata, intercostal long cells, prickles and macro-hairs. Examples of the variation in these structures are illustrated in Figures 1 and 2. The differences between species are summarized in Table 2, and below in the form of a dichotomous key.

Leaf anatomical key to the species of *Helictotrichon* in southern Africa (excluding *H. quinquesetum*) based on epidermal structures as seen in surface view

1a Macro-hairs (including crozier hairs) and prickles present:

2a Silica bodies equidimensional (vertical and horizontal dimensions approximately equal), round (circular in outline), fitting into concavities of cork cells:

- 3a Macro-hairs straight; square to rectangular paired intercostal cork-silica short cells situated between long cells ..... *H. roggeveldense* (Figure 2B)
- 3b Macro-hairs with apices hooked (crozier type); crescentic (enfolding the silica cell) paired intercostal cork-silica short cells situated between long cells ..... *H. rogerellisii* (Figure 2A)
- 2b Silica bodies horizontally elongated (horizontal dimensions greater than vertical dimensions), ends rounded and outlines sinuous:
  - 4a Macro-hairs with many, usually smaller, specialized epidermal cells associated with the base of the hair; intercostal long cells with moderately thickened walls and cuticular flanges well-developed .... *H. longum* (Figure 1F)
  - 4b Macro-hairs with one specialized epidermal cell associated with the base of the hair; intercostal long cells with unthickened walls and no cuticular flanges present ..... *H. galpinii* (Figure 1C)
- 1b Macro hairs absent; prickles present:
  - 5a Prickle base angular:
    - 6a Prickle barb short (less than the length of the base); costal short cells are silico-suberose couples (cork-silica cell pairs) with cork cells tall and narrow, and silica bodies not tall and narrow ..... *H. hirtulum* (not illustrated)
    - 6b Prickle barb medium (as long as or slightly longer than the base); costal short cells are silico-suberose couples (cork-silica cell pairs) with cork cells crescentic and enfolding the silica bodies ..... *H. longifolium* (Figure 1E)
  - 5b Prickle base elongated, oval or elliptic:
    - 7a Costal short cells silico-suberose couples with cork cells crescentic and enfolding the silica bodies:
      - 8a Intercostal long cells straight-walled without undulations:
        - 9a Prickles small (base shorter than the stomata) ..... *H. turgidulum* (Figure 2C & D)
        - 9b Prickles medium (base as long as or slightly longer than the stomata) ..... *H. dodii* (Figure 1B)
      - 8b Intercostal long cells irregular (slightly undulating), with moderately, or deeply undulating walls:
        - 10a Prickle barbs (shape in relation to base) not developed from the apex of the conical base and raised ..... *H. capense* (Figure 1A)
        - 10b Prickle barbs developed basally from the apex of the base, and slightly raised:
          - 11a Silica bodies elongated (horizontal dimension greater than vertical dimension), ends rounded and outlines smooth ..... *H. natalense* (Figure 1H)
          - 11b Silica bodies equidimensional (vertical and horizontal dimensions approximately equal), ends squarish or angular and outlines irregular ..... *H. leoninum* (Figure 1D)
    - 7b Costal short cells silico-suberose couples with cork cells tall and narrow but silica bodies not tall and narrow:
      - 12a Silica bodies equidimensional (vertical and horizontal dimensions approximately equal), ends square, outlines (shape) cubical or slightly rectangular ..... *H. barbatum* (not illustrated)
      - 12b Silica bodies elongated (horizontal dimensions greater than vertical dimensions), ends rounded, outlines (shape) sinuous or nodular:
        - 13a Silica bodies ends rounded and outlines (shape) nodular ..... *H. namaquense* (Figure 1G)
        - 13b Silica bodies ends rounded and outlines sinuous ..... *H. galpinii* (Figure 1C)

The variation in the characters used in describing the leaf epidermal anatomy of *Helictotrichon* and their taxonomic importance are highlighted below. Structures such as intercostal long cells, stomata, intercostal short cells, prickles, macro-hairs, silica bodies and costal cells are particularly useful for distinguishing between species (Table 2).

Intercostal long cells (Figure 2D)

The intercostal zone of the epidermis consists of two distinct sized cells. The larger cells are elongated horizontally and are relatively narrow vertically. These intercostal long cells can vary, in size, shape and undulations, vertically across a single intercostal zone (Figure 2D). Therefore the intercostal long cells adjoining the adjacent costal zone are often comparatively short and wide with markedly undulate walls and the long cells located centrally are longer and narrower with straighter walls (Ellis 1979).

The intercostal long cells of *H. turgidulum* and *H. dodii* have straight, not undulating walls. In *H. capense*, *H. leoninum* and *H. natalense* these cells are either irregular (slightly undulating), moderately, or deeply undulating. In *H. longum* walls of the intercostal long cells are moderately thickened and cuticular flanges are developed, whereas in *H. galpinii* the cell walls are unthickened with no cuticular flanges present.

Intercostal short cells (Figure 2C)

These cells, which generally alternate in horizontal rows with the much longer intercostal long cells are usually nearly equidimensional in shape. The silico-suberose couples or cork-silica cell pairs are intercostal short cells that occur in pairs; other short cells are solitary. For diagnostic purposes the frequency of the occurrence of short cells and the contrasting of their presence in the costal and intercostals zones are worth considering (Ellis 1979).

The basal member of the short cell pair is always the cork cell or suberous cell, whether it is a silico-suberose couple or not. A brief description of the changes that characterize the primary stages of differentiation of the cork-silica cell pairs was not studied in *Helictotrichon*, although these microscopic changes give a better understanding of the development of these taxonomically very important silica bodies (Ellis 1979).

Intercostal short cells in the material studied are paired short cells situated between long cells, and show some interspecific variation. The paired short cells in *Helictotrichon capense*, *H. dodii*, *H. longifolium*, *H. natalense* and *H. rogerellisii* are silico-suberose couples or cork-silica cell pairs and are crescentic, enfolding the silica cell, whereas those of *H. barbatum*, *H. leoninum* and *H. roggeveldense* are square to rectangular in shape.

Stomata (Figure 2D)

The subsidiary cells, as seen in surface view, can be used to classify grass stomatal complexes, which are located in the intercostals zones. To describe the stomatal complexes of Poaceae, the following terms are needed (Stace 1965; Ellis 1979).

The dome-shaped subsidiary cell type is referred to as ovoid, while the parallel sided type is rectangular. In Poaceae, the stomata are confined to the intercostal zones, which may, depending on the species, include one or more stomatal bands and each band may include one or more rows of stomata.



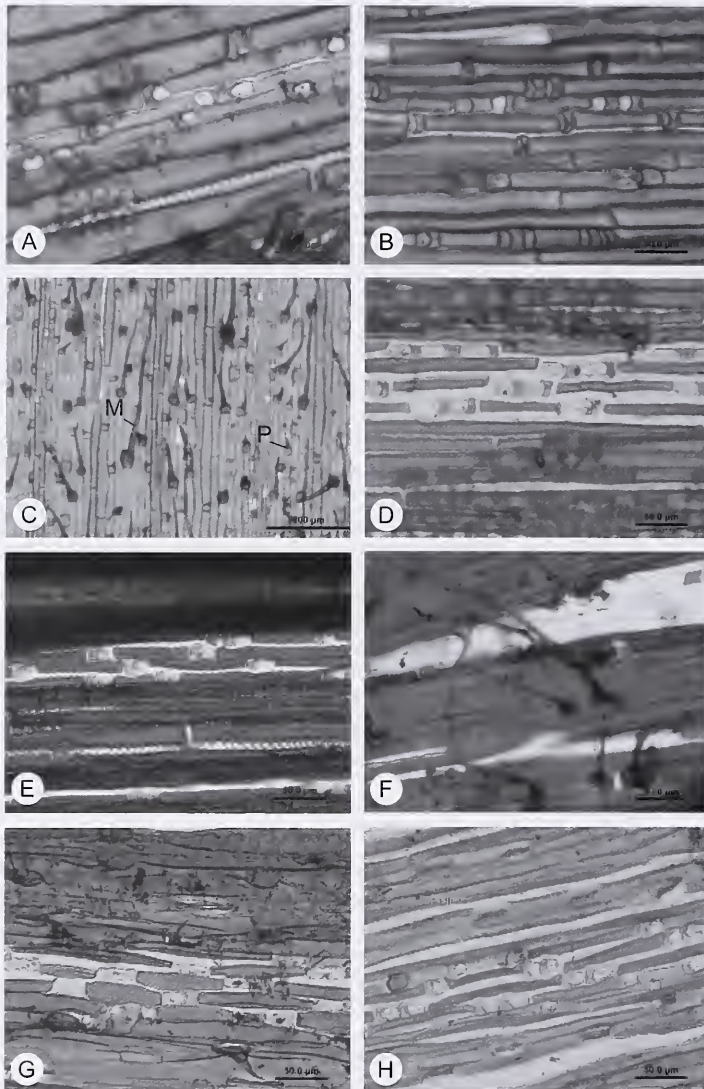


FIGURE 1.—Epidermal structures in *Helictotrichon*. A, *H. capense* (Story 3803); B, *H. dodii* (Pole-Evans 499); C, *H. galpinii* (Ellis 1389), P, prickle, M, macro-hair; D, *H. leoninum* (Ellis 225); E, *H. longifolium* (Davidse 6962); F, *H. longum* (Acocks 20691); G, *H. namaquense* (Ellis 5997); H, *H. natalense* (Rennie 1534).

In all the *Helictotrichon* species studied, the stomata are either dome-shaped, that is the subsidiary cells are rounded, or have parallel-sided subsidiary cells so that they are rectangular in outline; or the stomatal complex is long and narrow. *Helictotrichon capense* and *H. dodii* stomata are tall dome-shaped as the vertical width of the subsidiary cells is greater in relation to the horizontal length. The rest of the species investigated have parallel-sided subsidiary cells.

#### Costal short cells (Figure 2C)

Usually the costal short cells are not the same shape or arranged in the same manner as those of the intercostal zones. It is therefore important in comparative work to ensure that there is no confusion by comparing intercostal short cells with costal short cells. Although the morphology of the costal short cells appears to be generally taxonomically more important than that of the intercostal short cells (Ellis 1979), both were examined in the present study.

When comparing the horizontal arrangement of the costal short cells, it was found that *H. capense*, *H. dodii*, *H. leoninum*, *H. longifolium*, *H. natalense*, *H. rogerellisii*, *H. roggeveldense* and *H. turgidulum* have silico-suberose couples with cork cells crescentic and enfolding the silica bodies. On the other hand, *H. barbatum*, *H. galpinii*, *H. hirtulum*, *H. longum* and *H. namaquense* have costal short cells where the silico-suberose couples have cork cells tall and narrow but the silica bodies are not tall and narrow (in comparison to those where the cork cells are the same shape as the silica bodies).

#### Prickles (Figure 1C)

These arise directly from, and form an integral part of the epidermis and are tough, shortly pointed structures with swollen bases and short, sharp spines or barbs. The relative differences in size and length of their barbs and bases are mainly used to distinguish different types of prickles:



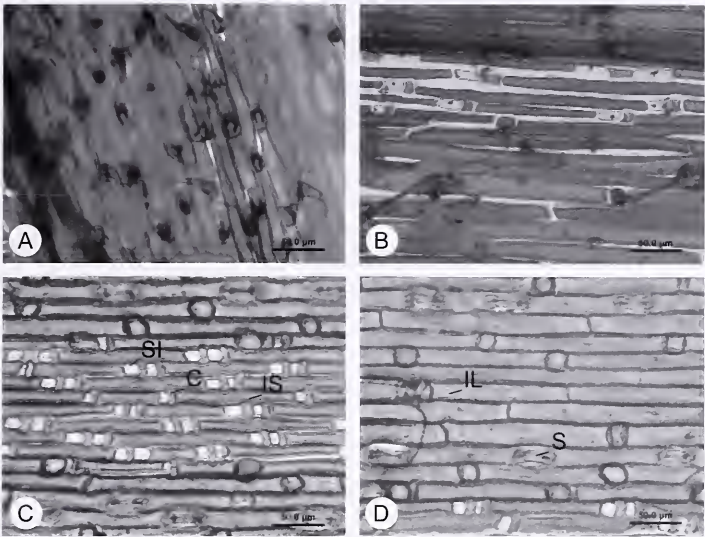


FIGURE 2.—Epidermal structures in *Helictotrichon*. A, *H. rogerellisii* (Ellis 4663); B, *H. roggeveldense* (Acocks 17178); C, *H. turgidulum* (Spies 3953); D, *H. turgidulum* (Spies 3953). SI, silica body, C, cork cell, IS, intercostal short cell, S, stoma; IL, intercostal long cell.

TABLE 2.—Characters used in describing the leaf epidermal anatomy of *Helictotrichon*

Species	Leaf epidermal characters													
	1		2		3		4		5		6		7	
	Intercostal long cells		Intercostal short cells		Stomata		Prickles		Macro-hairs		Silica bodies		Costal short cells	
	1a	1b	2a	2b	3a	3b	4a	4b	5a	5b	6a	6b	7a	7b
<i>H. barbatum</i>	X			X		X		X				X		X
<i>H. capense</i>		X	X		X			X				X	X	
<i>H. dodii</i>	X		X		X			X				X	X	
<i>H. galpinii</i>	X					X		X		X	X			X
<i>H. hirtulum</i>		X				X	X				X			X
<i>H. leoninum</i>		X		X		X		X				X	X	
<i>H. longifolium</i>		X	X			X	X					X	X	
<i>H. longum</i>	X					X				X	X			X
<i>H. namaquense</i>	X					X		X			X			X
<i>H. natalense</i>		X	X			X		X			X		X	
<i>H. roggeveldense</i>		X		X		X				X		X	X	
<i>H. rogerellisii</i>		X	X			X			X			X	X	
<i>H. turgidulum</i>	X					X		X				X	X	

1 = Intercostal long cells:  
1a = walls straight not undulating.  
1b = walls either irregular (slightly undulating), moderately, or deeply undulating.

2 = Intercostal short cells:  
2a = silico-suberose couples or cork-silica cell pairs are crescentic, enfolding the silica cell.  
2b = silico-suberose couples or cork-silica cell pairs are square to rectangular in shape.

3 = Stomata:  
3a = are tall dome-shaped as the vertical width of the subsidiary cells is greater in relation to the horizontal length.  
3b = subsidiary cells are parallel-sided.

4 = Prickle base:  
4a = base angular.  
4b = base elongated, oval or elliptic.

5 = Macro-hairs:  
5a = apices hooked and known as crozier hairs.  
5b = with single or many, usually small specialized epidermal cells associated with the base of the hairs.

6 = Silica bodies:  
6a = elongated (horizontal dimension greater than vertical dimension).  
6b = equidimensional (vertical and horizontal dimensions approximately equal).

7 = Costal short cells:  
7a = have silico-suberose couples with cork cells crescentic and enfolding the silica bodies.  
7b = the silico-suberose couples have cork cells tall and narrow but the silica bodies are not tall and narrow.

X = Character state present.

Prickles have elongated, oval or elliptical bases and are usually larger than hooks.

The angular prickles of the leaf margin comprise a distinct group and usually differ from the typical prickles occurring elsewhere on the same leaf.

The relative proportions of the barb length to the base size are gauged by projecting parallel lines through the apex of the barb and the opposite ends of the prickly hair base. The base size is assessed, in this study, by comparing it with the length of the stomata on the same leaf (Ellis 1979).

Barb size estimated by comparison with the length of the base: *Helictotrichon hirtulum* and *H. longifolium* both have the prickly base angular, but differ from one another in that the prickly barbs are shorter than the length of the base (short barb) in *H. hirtulum*, whereas in *H. longifolium* the prickly barbs are as long as or slightly longer than the base (medium barb length).

Base size estimated by comparison with the length of the stomata: *H. turgidulum* has small prickles (the base is shorter than the stomata), while in *H. dodii* the prickles are medium-sized (the base is as long as or slightly longer than the stomata).

Barb shape in relation to the base: When using this character it was found that *H. capense* has prickly barbs that are not developed from the apex of the conical base and are raised, while *H. leoninum* and *H. natalense* have prickly barbs developed basally from the apex of the base and slightly raised.

#### Macro-hairs (Figure 1C)

These are much longer than micro-hairs and prickles, varying considerably in length, even on a single leaf, in flexibility, wall thickness and how far the bases are sunken between the surrounding epidermal cells. The different macro-hair types, such as the crozier and the type of epidermal cells associated with the base of the hair, are taxonomically significant. These hairs arise from conical bases in the intercostal zones (Ellis 1979).

*Helictotrichon rogerellisii* has a specialized type of macro-hair with hooked apices known as crozier hairs, while the following have straight macro hairs and are distinguished from each other as follows: in *H. longum* the macro-hairs have many, usually small, specialized epidermal cells associated with the base of hair; *H. galpinii* and *H. roggeveldense* have macro-hairs with a single specialized epidermal cell associated with the base of the hair.

#### Silica bodies (Figure 2C)

Silica bodies, found in specialized epidermal cells, are discrete deposits of hydrated silica. This term is distinct from the term opal phytolith, which includes silica deposits sometimes present in other epidermal cells (Ellis 1979).

The shapes of typical silica bodies are very important taxonomically as they are characteristic for species (Ellis 1979). However, note that the shapes of the silica

cells are not necessarily the same as the outlines of the silica bodies in which they are located. Various shapes of silica bodies have been recognized such as round, oval, oblong, linear, squarish or rectangular, as well as crescent-shaped or half-moon (Ellis 1979). In *Helictotrichon*, the shapes of silica bodies, which are normally described as seen in surface view, are round, squarish or rectangular.

The *Helictotrichon* species investigated here show a variety of silica bodies. *H. galpinii*, *H. hirtulum*, *H. longum*, *H. namaquense* and *H. natalense* have silica bodies that are elongated (horizontal dimension greater than vertical dimension); but they differ from one another in that those of *H. natalense* have rounded ends and smooth outlines; in *H. namaquense* the ends are rounded and the outline or shape nodular; and in *H. galpinii*, *H. hirtulum* and *H. longum* they have rounded ends and a sinuous outline.

*Helictotrichon barbatum*, *H. leoninum*, *H. rogerellisii* and *H. roggeveldense* all have silica bodies that are equidimensional (vertical and horizontal dimensions approximately equal). Those of *H. leoninum* have squarish or angular ends with irregular outlines, *H. barbatum* has square, cubical or slightly rectangular ones, whereas those of *H. rogerellisii* and *H. roggeveldense* are round (circular in shape), fitting into the concavities of the cork cells.

#### CONCLUSIONS

New studies of the genus *Helictotrichon* in southern Africa were necessary because much work is being done worldwide on the delineation of the genus, but hitherto little has been done on the southern African species (Mashau *et al.* 2010). Members of the genus in southern Africa are difficult to separate into species based on morphological characters alone. The anatomical features of the grass leaf epidermis have proved to be very useful in helping delimit the species and should be used in addition to the morphological characters.

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## HYACINTHACEAE

### NOMENCLATURAL CORRECTIONS IN SUB-SAHARAN AFRICA, PREDOMINANTLY SUBFAM. URGINEOIDEAE

The recent publication of a checklist of the flowering plants of sub-Saharan Africa by Klopper *et al.* (2006) represents a major consolidation of taxonomic information from across the region. An added benefit is that it highlights names that are still lacking combinations in genera that have been recircumscribed in recent revisions. Such instances pose an impediment to consistent checklists for the continent and for herbarium curation. Hyacinthaceae are one such instance. Generic circumscriptions in the family have been significantly and often substantially altered in the last few decades and several tropical taxa have been overlooked in the process. Here we address species treated by Klopper *et al.* (2006) in genera of predominantly subfamily Urgineoideae, one of the three subfamilies of Hyacinthaceae represented in Africa (Speta 1998b; Manning *et al.* 2004). The fourth subfamily Oziroëoideae is restricted to South America.

The generic classification of Urgineoideae has been discussed elsewhere (Speta 1998b; Manning *et al.* 2004). Whatever the competing merits of the available systems, the synthetic classification recognising just the two genera *Bowiea* Harv. ex Hook.f. (1 sp.) and *Drimia* Jacq. ex Willd. ( $\pm 100$  spp.) is currently the only practicable one, and has been most fully implemented in continental Africa and Madagascar (Manning *et al.* 2004; Pfosser *et al.* 2006; Wetschnig *et al.* 2007). Although Klopper *et al.* (2006) adopted this system, they were forced to implement it only partially and somewhat inconsistently by having to accommodate those names, largely west-tropical African, lacking combinations in *Drimia*. Consequently, they still list 21 species under *Urginea* Steinh., although this genus has long since been subsumed within *Drimia* (Jessop 1977), plus two names each under *Schizobasis* Baker and *Thuranthos* C.H. Wright. Less explicity, they duplicate some entries under the generic names *Charybdis* Speta and *Ebertia* Speta.

Here we examine the names listed by Klopper *et al.* (2006) under the genera *Charybdis* (1 sp.), *Ebertia* (2 spp.), *Schizobasis* (2 spp.), *Thuranthos* (2 spp.) and *Urginea* (21 spp.), and provide the appropriate taxonomic conclusions where possible, following the classification of the family proposed by Manning *et al.* (2004) [subfamilies Hyacinthoideae and Urgineoideae] and Manning *et al.* (2009) [subfamily Ornithogaloideae]. It

is an extraordinary fact that taxa from all three of these subfamilies have been described as species of *Urginea* in the past. We are also able to correct some additional errors and oversights in the list, including duplications and overlooked synonyms. Of a total of 27 names that we considered, one is a new synonym of *Schizocarphus nervosus* (Burch.) Van der Merwe (Hyacinthoideae), six are new or existing synonyms in *Albuca* L. (Ornithogaloideae), nine are new or existing synonyms in *Drimia* (Urgineoideae), with an additional three new combinations in that genus, four are erroneous names, and the identities of a further four remain uncertain.

### ACCEPTED NAMES

#### Subfam. Hyacinthoideae

***Schizocarphus nervosus* (Burch.) Van der Merwe** in Flowering Plants of South Africa 23: t. 904 (1943). *Ornithogalum nervosum* Burch.: 537 (1822). *Scilla nervosa* (Burch) Jessop: 243 (1970). Type: South Africa, 'between Griquatown and Wittewater, Burchell 1968 (K, holo.—ALUKA image!).

*Urginea bragae* Engl. in Die Pflanzenwelt Ost-Afrikas C: 142 (1895), syn. nov. Type: Portuguese East Africa [Mozambique], Beira, *Braga s.n.* (B100167478, holo.—digital image!).

Examination of the type of this name confirms that it is in fact a narrow-leaved form of *Schizocarphus nervosus* (Burch.) Van der Merwe, which is widely distributed through subtropical Africa. The pilose peduncle and veins, and the fibrous neck on the bulb described in the protologue are highly diagnostic. An annotation label with the unpublished name *Schizocarphus bragae* affixed to the type of *Urginea bragae* by U. & D. Müller-Doblies is consistent with our generic placement. *S. nervosus* is, however, extremely variable in leaf shape and the type of *U. bragae* falls well within the variation accepted for the species.

#### Subfam. Ornithogaloideae

***Albuca nigritana* (Baker) Troupin** in Bulletin du Jardin botanique de l'État à Bruxelles 25: 231 (1955).



*Albuca ledermannii* Engl. & K.Krause: 143 (1910).

Klopper *et al.* (2006) overlooked the fact that *Albuca ledermannii* was treated as a synonym of *Albuca nigritana* by Hepper (1968).

***Albuca pulchra*** (Schinz) J.C.Manning & Goldblatt in Manning *et al.* in *Taxon* 58: 92 (2009). *Ornithogalum pulchrum* Schinz: 221 (1890).

*Urginea angolensis* Baker in *Journal of Botany* 12: 364 (1874), syn. nov. [non *Albuca angolensis* Welw. (1859)]. Type: 'Angola, in ditone Ambriz in sylvis', June 1873, *Monteiro & Monteiro s.n.* K000400581 (K, holo.—ALUKA image!).

Examination of the type of *Urginea angolensis* confirms that the long, linear-lanceolate bracts, specified as unspurred in the protologue (Baker 1874), do indeed lack the basal spurs characteristic of Urgineoideae and that the species is misplaced in the genus and subfamily. The depressed-globose capsules with large, disc-like seeds, and the free, subsimilar tepals with veins congested along the midline place the species in *Albuca* subg. *Namibiogalum* (= *Battandiera* Maire *fide* Martínez-Azorín *et al.* 2011) (Ornithogaloideae). We conclude that it represents a form of *Albuca pulchra* with slightly shorter pedicels than usual. Although recorded from Angola by Obermeyer (1978), *A. pulchra* was not included in the recent checklist for that country (Figueiredo & Smith 2008).

Although *Urginea angolensis* is the earliest name for the species, the existence of *Albuca angolensis* Welw. (1859) precludes its transfer to that genus.

***Albuca sudanica*** A.Chev. in *Mémoires de la Société Botanique de France* 2: 93 (1908).

*Albuca garuensis* Engl. & K.Krause: 144 (1910).

*Albuca stricta* Engl. & K.Krause: 144 (1910).

*Urginea garuensis* Engl. & K.Krause: 147 (1910).

*Albuca garuensis*, *A. stricta* and *Urginea garuensis* were all treated as synonyms of *Albuca sudanica* by Hepper (1968), a treatment overlooked by Klopper *et al.* (2006).

***Albuca virens*** (Ker Gawl.) J.C.Manning & Goldblatt in Manning *et al.* in *Taxon* 58: 93 (2009). *Ornithogalum virens* Ker Gawl.: sub t. 814 (1824) [= *Ornithogalum tenuifolium* Redouté sensu Obermeyer 1978]. Type: Mozambique, Delagoa Bay, *Forbes s.n.* K000365579 (K, holo.—ALUKA image!).

*Ornithogalum flavovirens* Baker: 366 (1874). *Urginea flavovirens* (Baker) Weim.: 442 (1937). *Stellarioides flavovirens* (Baker) Speta: 173 (2001). Lectotype, designated by Obermeyer: 361 (1978): South Africa, [Eastern Cape], near Somerset East, *MacOwan* 1852 (K, lecto.—ALUKA image!; BOL, GRA, iso.).

*Urginea flavovirens* is a later combination of *Ornithogalum flavovirens*, treated by Obermeyer (1978) as a synonym of *Ornithogalum tenuifolium* Redouté [now

*Albuca virens* (Manning *et al.* 2009)]. We have seen the type and concur with Obermeyer's opinion.

Subfam. Urgineoideae

***Drimia altissima*** (L.f.) Ker Gawl. in Curtis's Botanical Magazine 27: t. 1074 [excl. illustration] (1808). *Ornithogalum altissimum* L.f.: 199 (1782). Type: South Africa, 'Cap. bonae spei', *Thunberg s.n.* UPS-THUNB8275 (UPS-THUNB, holo.—microfiche!).

*Ornithogalum giganteum* Jacq.: 45, t. 87 (1797). *Urginea gigantea* (Jacq.) Oyewole: 167 (1975). Type: Illustration in Jacquin, *Plantarum rariorum horti caesarei schoenbrunnensis* 1: t. 87 (1797).

Although *Ornithogalum giganteum* has been consistently treated as a synonym of *Drimia altissima* (Ker Gawl. 1808; Hutchinson 1936; Jessop 1977; Obermeyer 1978), Oyewole (1975) favoured the recognition of both *D. altissima* (as *Urginea altissima*) and *U. gigantea* based on his studies in Nigeria. *D. altissima* is so widely distributed through Africa that any meaningful recognition of segregates can only take place in the context of its entire distribution.

***Drimia calcarata*** (Baker) Stedje in *Nordic Journal of Botany* 7: 663 (1987). *Ornithogalum calcaratum* Baker: 723 (1872a). Lectotype, designated by Stedje: 663 (1987): Illustration from a living plant sent from South Africa, Eastern Cape by *MacOwan* (K, lecto.—ALUKA image!).

*Urginea modesta* Baker: 6 (1892). *Drimia modesta* (Baker) Jessop: 302 (1977). Type: South Africa, 'Pondoland', *Bachmann* 273 (K, holo.).

*Urginea nyasae* Rendle in *Transactions of the Linnean Society of London*, ser. 2, Botany, 4(1): 50 (1894), syn. nov. Type: Malawi, 'Milanjii, 6 000 ft.', Oct. 1891., *Whyte s.n.* BM000911782 (BM, lecto.—ALUKA image!, designated here). [Syntype: 'Nyasa-land', 1891, *Buchanan* 998 BM000911783 (BM, syn.—ALUKA image!).] [The Whyte collection is selected as the lectotype as being the most complete, including flowers and seeds].

*Urginea umgeniensis* Poelln.: 209 (1944), as nom. nov. pro *U. pauciflora* Baker: 786 (1901), hom. illegit. non Baker: 539 (1898). Type: South Africa, 'Natal, Umgeni Falls', *Rehmann* 7455 (Z, holo.).

*Urginea nyasae* was overlooked by Stedje (1987, 1996) in her treatment of *Drimia* for East Africa. We have examined the type material and conclude that it is conspecific with *D. calcarata*. The filiform leaf, slender inflorescence of small flowers, long spurs on the lower bracts, and the fusiform seeds with reduced wings are diagnostic for that species.

*Urginea umgeniensis* was regarded as a synonym of *Drimia modesta* by Jessop (1977) in his revision of the South African species and the species was in turn considered to be a synonym of *Drimia calcarata* (Stedje 1987), a treatment overlooked by Klopper *et al.* (2006).

***Drimia glaucescens*** (Eugl. & K.Krause) H.Scholz in *Bulletin du Muséum National d'Histoire Naturelle Sec-*

tion B, *Adansonia*, Sér. 4, 11(4): 444 (1990). *Urginea glaucescens* Engl. & K.Krause: 146 (1910).

*Urginea paludosa* Engl. & K.Krause: 146 (1910).

*Urginea ensifolia* (Thonn.) Hepper: 497 (1968).

*Urginea paludosa* was treated by Hepper (1968) as a synonym of *Urginea ensifolia* (Thonn.) Hepper. The transfer of this epithet to *Drimia* is prevented by the earlier *D. ensifolia* Eckl., and Scholz (1990) accordingly provided the new combination *D. glaucescens* based on the next available name, *Urginea glaucescens* Engl. & K.Krause.

***Drimia indica* (Roxb.) Jessop** in Journal of South African Botany 43: 272 (1977). *Scilla indica* Roxb.: 147 (1824). Lectotype, designated by Deb & Dasgupta: 118 (1974): India, Coromandel, *Roxburgh s.n.*, illustration t. 1821 (CAL, lecto., not seen).

*Urginea zambesiaca* Baker in Journal of the Linnean Society, Botany 13: 223 (1872a), syn. nov. *Thuranthos zambesiacum* (Baker) Kativu in Kativu & Drummond: 113 (1994). Type: Mozambique, 'lower Zambesi, near expedition Island', *Kirk* 128 (K, holo., not seen).

*Urginea salmonea* Berhaut in Flore du Senegal, ed. 2: 428 (1967), syn. nov. Type: Senegal, Mbao, 16 Jun. 1954, *Berhaut* 1682 (P, holo.—ALUKA image!; P, iso.—ALUKA image!).

*Urginea zambesiaca* was distinguished from *Drimia indica* by its slightly longer style and obtuse capsules (Baker 1872a). Although often confused with *Drimia macrocarpa* Stedje, the type of *Urginea zambesiaca* Baker was considered by Stedje (1996) to fall within the range of variation of *Drimia indica*, although she did not formally treat it as a synonym of that species. We remedy this omission here.

The type of *Urginea salmonea* is part of the widespread and variable *Drimia indica* complex. It was diagnosed by Berhaut (1967) on minor morphological grounds (ovary size and leaf apex shape) against *U. sebirei* Berhaut, a species that is now treated as conspecific with *D. indica*. The morphological and cytological variation among Nigerian populations of *D. indica* was extensively studied by Oyewole (1987a,b), who concluded that the species comprises a stable polymorphism in which different morpho- and ecotypes attained some level of reproductive isolation and genetic stability. Detailed genetic studies are clearly a prerequisite for any meaningful understanding of patterns of variation in the species. Pending this, we consider it prudent to provisionally treat *U. salmonea* as a synonym of *D. indica*.

***Drimia intricata* (Baker) J.C.Manning & Goldblatt** in Goldblatt & Manning, Strelitzia 9: 712 (2000). *Anthericum intricatum* Baker: 140 (1872b). *Schizobasis intricata* (Baker) Baker: 140 (1874). Lectotype, designated by Stedje & Thulin: 600 (1995): South Africa, without locality. *Zeyher* 4284 (K, lecto.; SAM, isoleccto!).

*Schizobasis angolensis* Baker in Transactions of the Linnean Society of London, Botany 1: 255 (1878), syn. nov. Type: Angola, 'Pungo Andongo, ad rupes ipsius

Praesidis', *Welwitsch* 3866 K000257004 (K, holo.—ALUKA image!).

*Schizobasis gracilis* R.E.Fr. in *Wissenschaftliche Ergebnisse der Schwedischen Rhodesia-Kongo-Expedition 1911–1912* 1: 227 (1916), syn. nov. Type: 'Nordost-Rhodesia, Kalungwesi-river, in Felsenritzen im Trockenwald, *Friese* 1157 (holo, not located).

*Drimia intricata*, as currently circumscribed, is a highly variable species with a wide distribution through Africa, including Angola (Stedje 1996), and with several current synonyms (Jessop 1977). It is possible that segregates should be recognised, but this can only be done when the species is reviewed across its entire range. In the interim it seems gratuitous to transfer the names *Schizobasis angolensis* and *S. gracilis* to *Drimia* and we accordingly place them in provisional synonymy. Both types fall within the range of variation currently accepted for the species as circumscribed by Jessop (1977) under the name *Schizobasis intricata* (Baker) Baker.

***Drimia johnstonii* (Baker) J.C.Manning & Goldblatt**, comb. nov. *Urginea johnstonii* Baker in Flora of Tropical Africa 7: 539 (1898). Type: 'Angola, near the river Cunene', Sept. 1883, *Johuston s.n.* K000400576 (K, holo.—ALUKA image!).

The small, caducous bracts and thin-textured perianth are consistent with the placement of this species in *Drimia*. The absence of spurs on the bracts mentioned by Baker (1898) in the protologue is not surprising given that the lower bracts have fallen—often only the lower bracts in the raceme are spurred in species of *Drimia*. The type of *U. johnstonii* was later annotated by Milne-Redhead on the sheet as indistinguishable from *Urginea brachystachys* Baker, now *D. brachystachys* (Baker) Stedje, from Tanzania and Ethiopia. This remains to be confirmed.

***Drimia minuta* J.C.Manning & Goldblatt**, nom. nov. pro. *Drimia nana* (Oyewole) J.C. Manning & Goldblatt in Manning *et al.* in Edinburgh Journal of Botany 60: 557 (2004), hom. illegit. non *D. nana* (Snijman) J.C.Manning & Goldblatt: 111 (2003). *Urginea nana* Oyewole: 623 (1989). *Ebertia nana* (Oyewole) Speta: 68 (1998a). Type: Nigeria, near the academic area, University of Ilorin, *S00/2111* (IUH, holo.; FHI, iso.).

The combination *Drimia nana* (Oyewole) J.C. Manning & Goldblatt (Manning *et al.* 2004) for the Nigerian species *Urginea nana* Oyewole is an illegitimate later homonym of the Namaqualand taxon *D. nana* (Snijman) J.C.Manning & Goldblatt (2003). We provide a replacement name here.

***Drimia psilostachya* (Welw. ex Baker) J.C.Manning & Goldblatt**, comb. nov. *Urginea psilostachya* Welw. ex Baker in Transactions of the Linnean Society of London, ser. 2, Botany 1(5): 247 (1878). Type: Angola, 'Cazengo in dumetis siccis arenosis', *Welwitsch* 3807 (BM, K, syn.—ALUKA images!).

The bracts are described as calcarate by Baker (1878) and we confirm this condition on the type and its place-



ment in *Drimia*. Its specific status remains to be investigated.

***Drimia simensis*** (Hochst. ex A.Rich.) Stedje in Nordic Journal of Botany 15: 597 (1995). *Scilla simensis* Hochst. ex A.Rich.: 327 (1850). *Urginea simensis* (Hochst. ex A.Rich.) Schweinf.: 291 (1867). *Charybdis simensis* (Hochst. ex A.Rich.) Speta: 60 (1998a).

Klopper *et al.* (2006) include this taxon twice, once as *Charybdis simensis* and again as *Drimia simensis*, uncertain that these names were combinations of the same epithet in different genera.

***Drimia sudanica*** Friis & Vollesen in Nordic Journal of Botany 19: 210 (1999), as nom. nov. pro *Urginea pauciflora* Baker: 539 (1898) [non *Drimia pauciflora* Baker (1892)]. *Ebertia pauciflora* (Baker) Speta: 68 (1998a). Type: Sierra Leone, 'near Wallia, on the River Scarcies', 11 Feb. 1892, Scott-Elliot 4580 K000400576 (K, holo.—ALUKA image!).

Klopper *et al.* (2006) include this taxon twice, once as *Ebertia pauciflora* and again as *Drimia sudanica*, unaware that they are alternate names for the same species in different genera.

***Drimia viridula*** (Baker) J.C.Manning & Goldblatt, comb. nov. *Urginea viridula* Baker in Flora of Tropical Africa 7: 538 (1898). Type: 'Congo, cultivated specimen', fl. in cult. 10 Sept. 1886, Bull s.n. K000257329 (K, holo.—ALUKA image!).

This taxon is treated as a distinct member of the *D. altissima* complex by Oyewole (1975). The spurred bracts and evanescent flowers of the type are consistent with the genus *Drimia*.

#### ERRONEOUS NAMES

'*Urginea brevifolia* Baker'. This name appears to be a typographical error for *Drimia brevifolia* Baker, a synonym of *Ledebouria revoluta* (L.f.) Jessop (Stedje & Thulin 1995).

'*Urginea fischeri* Baker'. This name appears to be a typographical error for *Drimia fischeri* Baker, a synonym of *Drimiopsis fischeri* (Engl.) Baker (Stedje & Thulin 1995).

'*Urginea hildebrandtii* Baker'. This name appears to be a typographical error for *Drimia hildebrandtii* Baker, a synonym of *Ledebouria kirkii* (Baker) Stedje & Thulin (Stedje & Thulin 1995).

'*Urginea angustisepala* Engl.' This name is a typographical error for *Drimia angustisepala* Engl., a synonym of *Ledebouria kirkii* (Baker) Stedje & Thulin (Stedje & Thulin 1995).

#### UNCERTAIN NAMES

We have been unable to locate type material to confirm the identity or generic placement of the following names.

***Urginea bequaertii*** De Wild. [as 'bequaerti'] in Plantae Bequaertianae 1: 31 (1921). Type: 'Belgian Congo, savane herbeuse, Bequaert 2768 (?BR, holo., not located).

The protologue makes no mention of the presence or absence of spurs on the bracts. Sofie De Smedt of the National Botanic Garden of Belgium confirmed that the type was not at BR in June 2012, but indicated that it might possibly be part of an undocumented loan that was outstanding at the time (De Smedt, pers. com. 26 June 2012). The bracts are described as 'lanceolate-linear, ... exceeding the buds and sometimes the flowers', which are greenish white with 'tepals 6–7 × 2.2 mm, brown on keel, with 3 veins'. The relatively large bracts are anomalous in *Drimia* and De Wildeman in fact compares the species to *Albucca abyssinica* in the protologue. We suspect that the name may well apply to a species of *Albucca*, possibly *A. virens*. A reference to *Ornithogalum tenuifolium* (now *Albucca virens*) made by Dominique Champluvier in 1987 on the species cover of *U. bequaertii* at BR is strong circumstantial support for this conjecture.

***Urginea brevipes*** Baker in Journal of Botany 12: 364 (1874). Type: 'Senegambia', Perrottet 782 ('Herb. DC.', holo., not located).

The protologue makes no mention of the presence or absence of spurs on the bracts. The type is noted by Baker (1874) to have been in 'Herb. DC.' Dr L. Gautier, Head Curator of Phanerogams at Geneva, confirmed it was not at G in June 2012, but indicated that it might possibly be part of an undocumented loan that was outstanding at the time (Gautier, pers. com. 8 June 2012).

***Urginea grandiflora*** Baker in Journal of the Linnean Society, Botany 13: 223 (1872a). Type: Sudan, 'in ditione Maris Rubri, Hor Tamanib, alt. 600 ped., Lord s.n. (holo., not located on ALUKA).

This species is known only from the type, collected on Jebel Tamanib, a mountain along the Red Sea near Samakin in northeast Sudan. Its identity remains unknown.

***Urginea insignis*** Engl. & K.Krause in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 45: 147 (1910). Type: 'Nord-Kamerun: bei Garua, in sandiger, teilweise steiniger und felsiger Gebüschsavanne', April 1909, Ledermann 3302, 3350 (†B, syn.).

Engler's herbarium was unfortunately lost (Staffeu & Cowan 1976) and the identity and correct generic placement of this name is unclear. Hutchinson (1936) was unable to account for this name in his treatment of the family for West Tropical Africa. Several of Engler & Krause's Cameroonian hyacinths have been shown by Hepper (1968) to be synonyms of other species and it is possible that this taxon, too, will prove to be conspecific with some other species.

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## CHENOPODIACEAE

### *CHENOLEA CONVALLIS*, A NEW SPECIES FROM WESTERN CAPE PROVINCE, SOUTH AFRICA

Generic circumscriptions in Chenopodiaceae have still to be fully resolved but modern treatments recognize four subfamilies, with subfamily Chenopodioideae segregated into six tribes (Kuhn *et al.* 1993). Keys to the genera of tribe Camphorosmeae in current use (Scott 1978; Kühn *et al.* 1993) rely heavily on fruit and seed characters to distinguish taxa, but the limited value of these characters for generic delimitation within the tribe has become increasingly apparent (Kadereit & Freitag 2011). This applies particularly to the form of appendages on the fruits that are likely to experience strong and variable selection for dispersal (Chu & Sanderson 2008). The most recent taxonomic conclusions of Kadereit & Freitag (2011) indicate that several genera, particularly *Bassia* All. and *Kochia* Roth, are highly polyphyletic and that the taxa fall within three clades corresponding with three informal groups, the *Chenolea* Thunb., *Sclerolaena* R.Br. and *Bassia* All./*Camphorosma* L. groups. The *Chenolea* group comprises five species of dwarf shrubs, perennial and annual plants placed in four widely disjunct genera, spread between Eurasia, western North America, southern Italy, and southern Africa. The *Sclerolaena* group, the largest of the three, incorporates a strictly perennial Australian group plus three annual species from Central Asia. The *Bassia*/*Camphorosma* group has a predominantly Eurasian geographic range but includes *B. dinteri* and *B. salsoloides* within southern Africa. The formal subtribal classification and supporting morphological data of these groups have not yet been published. Nevertheless, Kadereit & Freitag (2011) stress the importance of the internal morphology of leaves in providing phylogenetically informative characters. The *Bassia*/*Camphorosma* group has various types of Kranz anatomy indicative of  $C_4$ -photosynthetic pathways, whereas the *Chenolea* and *Sclerolaena* groups have non-Kranz anatomy, reflecting  $C_3$ -photosynthesis.

Plants of the monotypic *Chenolea* and the moderately sized genus *Bassia*, with which it has previously been combined (Scott 1978), are subshrubs or herbs with small bisexual, sometimes pistillate flowers, and slightly accrescent fruiting perianths. In common with other members of tribe Camphorosmeae, the seeds contain an annular or horseshoe-shaped embryo and moderately developed perisperm, the flowers lack bracteoles, and the stigmas are entirely papillose (Kadereit & Freitag 2011). Scott (1978) circumscribed *Bassia* to encompass both *Kochia* Roth and *Chenolea*, each with one species

in southern Africa, as well as the monotypic, Eurasian *Londesia* Fisch. & C.A.Mey. In contrast, the most recent molecular-based classification of Kadereit & Freitag (2011) treats *Bassia* as a strictly Afro-Eurasian genus of  $\pm$  20 species that includes *Londesia* and the major part of *Kochia*. *Chenolea*, which resolved separately in their analysis, was reinstated as a genus endemic to southern Africa's coast.

Recent plant checklists for southern African Chenopodiaceae (Makgaka 2003; Klopper *et al.* 2006) list four species of *Bassia* in the region, including *B. diffusa* (Thunb.) Kuntze, which is now treated in *Chenolea* as *C. diffusa* Thunb. Only two of the remaining three species are native to southern Africa: *B. dinteri* (Botsch.) A.J.Scott, a local endemic in the southern Namib of Namibia, and *B. salsoloides* (Fenzl) A.J.Scott, widespread in South Africa's Nama Karoo, extending from northern Bushmanland eastwards to the southern Free State and southwards through the Great Karoo. The third species, *B. indica* (Wight) A.J.Scott, appears to have been introduced from an area between North Africa and India (Scott 1978; Kadereit & Freitag 2011).

In 2011, Mrs A. le Roux, an ecologist undertaking a long-term study of the vegetation in the valley and hills surrounding the Greater Brandvlei Dam near Worcester, Western Cape, encountered several unusual plants of Chenopodiaceae in the area. Based on a study of the leaf anatomy in particular, notably the non-Kranz anatomy, we recognize them as representing an undescribed species belonging to the *Chenolea* group of Camphorosmeae with a fruiting perianth quite unlike any other species in the group. We discuss our interim decision to place this new species in the genus *Chenolea* with the name *C. convallis*, in reference to the secluded Brandvlei Valley where the plants are found.

For anatomical investigation, fresh material was fixed in FAA and then embedded in wax before sectioning and double-staining with alcian blue and safranin following Rudall (1995).

#### TAXONOMY AND CONSERVATION STATUS

***Chenolea convallis* Snijman & J.C.Manning, sp. nov.**

Like taxa in the *Chenolea* group *sensu* Kadereit & Freitag (2011) in its succulent,  $\pm$  opposite leaves with



non-Kranz anatomy of the *C<sub>3</sub> Neokochioid* or *Eokochoioid* type, but differing by the combination of a woody habit and the fruiting perianth with a prominent, succulent, rugose, pale brown, glistening dorsal tubercle below the apex of each lobe.

**TYPE.**—South Africa, Western Cape, **3319** (Worcester): Worcester District, Greater Brandvlei Dam area, slopes on E side of Dam, 212 m, (–CD), 23 February 2012, D. Snijman & A. le Roux 2368 (NBG, holo.; KASSEL, MO, PRE, iso).

Succulent-leaved, branching subshrub, up to 300 mm tall, resprouting from a deeply rooted, woody base. *Branches* mostly erect, slender, striate, young shoots sparsely villose. *Leaves* subopposite, sometimes appearing opposite, distantly spaced throughout, sometimes deciduous below, sessile, linear to narrowly lanceolate, 5–8 × 1.5–2.0 mm, almost semiterete, adaxially flattened, pale glaucous green, insertion on stem marked by a narrow brownish band, young leaves lightly pubescent with filiform, 1-seriate hairs on both surfaces, older leaves glabrescent, minutely granular from remnants of hair bases under a 10 × lens, each comprising a swollen basal cell and narrowly tubular distal cell directed towards apex, anatomy non-Kranz. *Inflorescence* resembling a terminal spike, up to 70 mm long, of up to 15 subopposite, axillary flower clusters. *Flowers* bisexual, 2 per axil (rarely with additional, aborted accessory flower), sessile, without bracteoles, protogynous; perianth campanulate, mostly 5-lobed, lobes ± ovate, ± 2.0–2.5 × 1 mm, connate for up to ± 1 mm, succulent, thinly villose, pale glaucous green, each with small, glabrous, dorsal tubercle below apex, margins membranous in distal third; stamens mostly 5, perigynous, shortly exserted, filaments slender, ± sigmoid, anthers dorsifixed, spreading horizontally at anthesis, broadly oblong-sagittate, 1.25 × 1.25 mm, apex ± smooth, dehiscence latrorse, pale yellow, pollen yellow; ovary ovoid, ± 0.5 × 0.5 mm, unilocular; ovule 1, basal; style short, stigmas 2, filiform, ± 0.75 mm long, entirely covered with papillae, reddish, well exserted prior to anthesis, ± withering thereafter. *Fruiting perianth* accrescent, free from pericarp, ± 4 mm diam., depressed-spherical, lobes dark and ± leathery, each ornamented distally with an enlarged, dorsal tubercle, tubercles succulent, rugose, 1.5 mm diam., pale brown and glistening, lobes below the tubercle shortly keeled, margins of lobes remaining narrowly membranous in distal third. *Fruit* an achene, with a membranous pericarp; mature seeds unknown. *Flowering period*: Feb. to Mar. Figure 1.

*Distribution and habitat*: *Chenolea convallis* is currently known from just one population near the foot of the west-facing slopes of the low hills on the eastern banks of the Greater Brandvlei Dam near Worcester, Western Cape (Figure 2). The plants, numbering no more than about 50 individuals, grow in stony loam, at approximately 212 m above sea level. The area lies on bedrock of the Witteberg Series, the youngest deposits of the Cape Supergroup and these are tilted towards the Breede River, which runs along the Worcester fault line. The soils of the hills are derived from shales and sandstones of the oldest formations of the Witteberg Series (Gresse & Theron 1992).

The surrounding vegetation, classified as Breede Shale Renosterveld (Rebello *et al.* 2006), includes succulent and asteraceous shrubs such as *Crassula tetragona* L. (Crassulaceae), *Elytropappus rhinocerotis* (L.f.) Less., *Eriocephalus africanus* L., *Helichrysum rutilans* (L.) D. Don, *Oedera genistifolia* (L.) Anderb. & K. Bremer, and *Pteronia ovalifolia* DC. (all Asteraceae). Some rare species found at the site are *Aspalathus muraltioides* Eckl. & Zeyh. (Fabaceae), *Phyllobolus caudatus* (L. Bolus) Gerbaulet (Aizoaceae) and two Iridaceae, *Moraea vivuzela* Goldblatt & J.C. Manning and *Sparaxis maculosa* Goldblatt. An average rainfall of ± 300 mm per annum falls mainly between May and August. *Chenolea convallis* is one of the few species in the Greater Brandvlei Dam area that flowers during the late summer drought, between February and March.

*Conservation status*: the current water level of the Greater Brandvlei Dam was reached in 1985 after successive enlargements to the dam in 1950 and 1972 (Le Roux *et al.* 2010), resulting in the inundation of the renosterveld, which now barely fringes the dam to the north and east. In effect, the rising water levels may already have been destroyed other suitable local habitats of *Chenolea convallis*. New proposals by the Department of Water Affairs to raise the water level of the Brandvlei Dam once again are further cause for concern about the future survival of *C. convallis*, given its close proximity to the present water's edge. According to the South African Red List categories and criteria (Raimondo *et al.* 2009) we suggest that *C. convallis* should be classified as Critically Endangered. It is noteworthy that prior to the collections made by Mrs. A. le Roux, *C. convallis* was not known in any of the major herbaria of South Africa (BOL, NBG, PRE, SAM) (acronyms after Holmgren *et al.* 1990).

## DISCUSSION

### Leaf anatomy

Leaves of Chenopodiaceae often exhibit specialized anatomy apparently related to the xeric and saline habitats favoured by the family (Metcalfe & Chalk 1965; Kühn *et al.* 1993; Kadereit *et al.* 2003). Those of *Chenolea convallis* are typical of many xeromorphic leaves (Figure 3), being thick and leathery, covered with a thick cuticle and apparently by wax layers. Slightly sunken stomata are scattered on both surfaces and are transversally oriented to the median vein as in all Chenopodiaceae (Figure 4). Internally, the mesophyll is isobilateral, with chloroplasts confined to three or four layers of palisade-like parenchyma on each side of the leaf. The middle of the leaf has about six layers of large, chloroplast-free, water-storage cells and a centrally situated vascular network, comprising one central bundle and five lateral bundles in the same median plane. In addition, two groups of smaller bundles join the outermost laterals on the abaxial leaf side. Only the central bundle is strengthened by a sclerenchyma cap abaxially. The small lateral veins are all oriented with the xylem facing out towards the chlorenchyma. This non-Kranz anatomy is a good match with the *Neokochioid* leaf type, illustrated by Carolin *et al.* (1975) and Chu & Sanderson (2008). It may also fit the leaf type briefly described for





FIGURE 1.—*Chenolea convallis*, Snijman & le Roux 2368 (NBG). A, part of plant showing resprouting habit; B, detail of striate stem showing subopposite leaves; C, part of inflorescence showing protogynous flowers: female phase; D, solitary flower at female phase; E, flowers: male phase; F, solitary stamen and gynoecium showing attachment, plus details of stamen showing dorsifixed anther; G, gynoecium (plus longitudinal section at lower magnification showing solitary, basal ovule); H, persistent fruiting perianth and achene, side view and from above. Scale bar: A, 10 mm; B–E, H, 1.5 mm; F, G, 0.5 mm. Artist: John Manning.

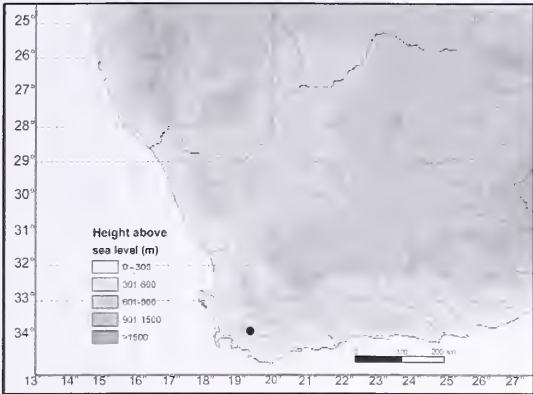


FIGURE 2.—Distribution of *Chenolea convallis*, ●.

*Eokochia* Freitag & G.Kadereit, but not yet illustrated (Kadereit & Freitag 2011). Both genera fall within the *Chenolea* group *sensu* Kadereit & Freitag (2011) of Camphorosmeae.

Leaf trichomes

Young leaves of *Chenolea convallis* are sparsely pubescent with appressed, three-celled, uniseriate, filiform hairs. The terminal cell of each hair is shed in the older, more succulent leaves, leaving only the swollen, thick-cuticled basal cell and narrow, tubular intermediate cell (Figure 4). Under a 10 × lens, these appear as small granules on the leaf surface. Similar trichomes have been described for many species of Camphorosmeae (Carolin 1983) and illustrated for *Neokochia americana* (S.Watson) G.L.Chu & S.C.Sand. (Chu & Sanderson 2008, Figure 2B) from North America and *Bassia muricata* (L.) Asch., distributed from Morocco to southern Iran (Metcalf & Chalk 1965, Figure 262A). *Chenolea diffusa*, in contrast, has more specialized, T-shaped hairs with a pluricellular stalk (Carolin 1983).

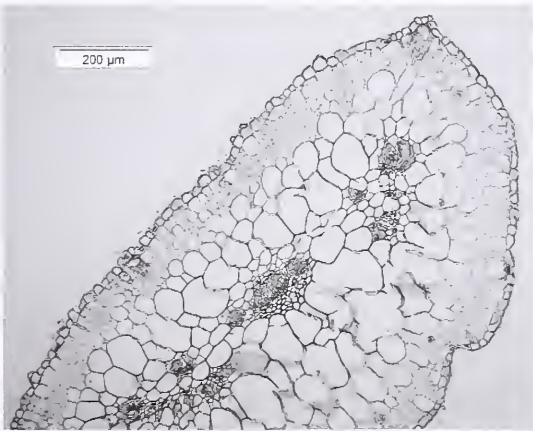


FIGURE 3.—*Chenolea convallis*, Snijman & le Roux 2368 (NBG). Transverse section of isobilateral leaf showing scattered, persistent, swollen, basal cells of partially shed trichomes on abaxial surface and vascular bundles arranged in the same median plane within water storing tissue in the middle of the leaf. Scale bar = 200 μm.

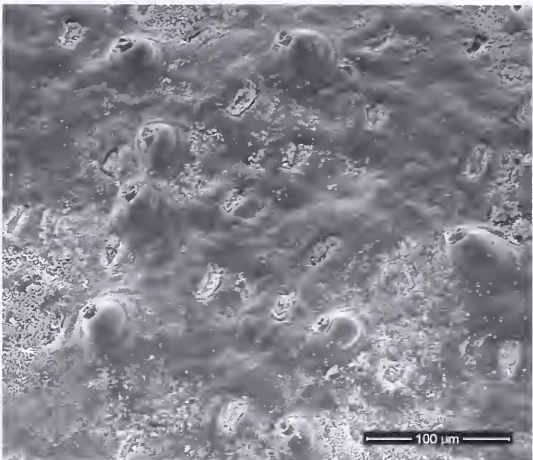


FIGURE 4.—*Chenolea convallis*, Snijman & le Roux 2368 (NBG). Detail of abaxial leaf surface showing sunken stomata and persistent swollen bases of uniseriate trichomes. Scale bar = 100 μm.

Fruiting perianth

*Chenolea convallis* is distinguished from other African species of Camphorosmeae by the unusual fruiting perianth, which develops prominent, wart-like, dorsal outgrowths below the apex of each lobe. Contrasting with the mostly dark-coloured, somewhat leathery fruiting lobes, the dorsal outgrowths are pale brown, glistening and irregularly sculptured. This morphology is also unique amongst taxa of the *Chenolea* group *sensu* Kadereit & Freitag (2011). *Chenolea diffusa* has smooth, fleshy, somewhat cowl-shaped fruiting perianth lobes, *Spirobassia* Freitag & G.Kadereit has three, obtuse perianth appendages, *Neokochia* (Ulbrich) G.L.Chu & S.C.Sand. has five, free, wing-like appendages from the base of the lobe and *Eokochia* has a five-winged perianth.

Harvester termites, *Microhodotermes viator*, have been seen gathering and carrying fallen twigs and leaves of *C. convallis* into holes at the base of several plants and it may be that the fruits are dispersed in this way, although probably not exclusively so.

Classification

This new species is easily identified by opposite to subopposite leaves and the distinctive fruiting perianth, which develops a large wart-like, dorsal outgrowth below the apex of each lobe. Based on the non-Kranz leaf morphology it shows a strong alliance with taxa in the *Chenolea* group (*sensu* Kadereit & Freitag 2011), in which only *Neokochia* is not monotypic. According to the classification proposed by Kadereit & Freitag (2011) and which is based heavily on molecular data and leaf anatomy, this new taxon may eventually warrant recognition as a new genus in the *Chenolea* group, but this requires further molecular investigation throughout the tribe. Since some of the relationships among the monotypic genera in this group are still unclear and because intercontinental disjunctions have been invoked to support their separation, our interim decision is to place this



new species in the southern African genus *Chenolea*, a name which takes precedence over all others in this group.

The addition of *C. convallis* to the previously monotypic *Chenolea* requires expansion of the generic description only to the extent of adding the subshrubby habit to the otherwise low, decumbent, straggling, near perennial habit of the plants, increasing the number of flowers per axil from one to two, extending the fruiting perianth morphology to include the presence of warty dorsal outgrowths on the lobes and adding the presence of simple, uniseriate hairs to the trichome types. In other genera of the tribe, such as *Bassia* (*sensu* Kadereit & Freitag 2011), characters such as growth form and perianth appendages also vary among species.

Apart from major leaf anatomical differences between *Chenolea sensu lato* and *Bassia* (non-Kranz vs. Kranz), *Chenolea* can be distinguished from the native species of *Bassia* in southern Africa by subtle differences in leaf arrangement, subopposite, sometimes distant leaves in *Chenolea* and alternate, often tightly clustered leaves in *Bassia*.

#### Additional specimens examined

WESTERN CAPE.—3319 (Worcester): Worcester, Greater Brandvlei Dam, 217 m, (–CB), 21 February 2011, *A. le Roux* 910 (NBG), 2 June 2011, *A. le Roux* 910a (NBG).

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#### THYMELAEACEAE

#### *LASIOSIPHON RIGIDUS*, A NEW SPECIES FROM THE TANKWA KAROO AND TWO NEW COMBINATIONS IN THE GENUS FOR SOUTH AFRICA

Thymelaeaceae are well represented in southern Africa, with ± 190 species in nine genera (Bredenkamp & Beyers 2000; Beaumont *et al.* 2009). Preliminary phylogenetic analyses of nuclear and plastid DNA

sequences (Van der Bank *et al.* 2002; Beaumont *et al.* 2009) indicate the need for substantial revision in the generic circumscriptions in subfamily Thymelaeoideae. This is especially evident in the large and diverse



genus *Gnidia* L., with > 140 spp. in tropical and southern Africa and Madagascar. *Gnidia* is evidently highly polyphyletic as currently circumscribed and is represented by at least four distinct lineages scattered throughout the Thymelaeoideae. As a first step towards a monophyletic generic classification of the subfamily, Beaumont *et al.* (2009) reinstated the genus *Lasiosiphon* Fresen., originally distinguished from *Gnidia* and allied tetramerous genera by its pentamerous flowers but subsequently included within *Gnidia* by Petersen (1959, 1978) on account of the evident instability of this character. Molecular analyses retrieved a monophyletic *Lasiosiphon* clade (comprising all pentamerous species of *Gnidia sensu lato* plus some tetramerous species) that was separated from the remaining *Gnidia* species by a well-supported clade comprising the genera *Dirca* L., *Ovidia* Raf., *Peddiea* Harv. and *Stephanodaphne* Baill. (Beaumont *et al.* 2009). Secondary characters diagnostic for *Lasiosiphon* are the capitate, involucre inflorescences subtended by foliaceous or petaloid bracts, the pubescent hypanthium, and the waxy, bright yellow to orange or red hypanthium lobes. With the inclusion of tetramerous species, the genus is diagnosable only by a combination of characters. Like *Gnidia*, it also includes some species with ebracteate, few-flowered inflorescences plus taxa with and without petaloid scales in the mouth of the hypanthium (Beaumont *et al.* 2009). *Lasiosiphon* currently numbers some 35 spp. from Africa and Madagascar, with  $\pm 20$  recorded from southern Africa (Wright 1915).

Here we describe a distinctive new species of *Lasiosiphon* endemic to the Tankwa [Tanqua] Karoo, previously misidentified and illustrated as *Gnidia microphylla* Meisn. (Van der Merwe 2010). It is distinguished by its rigid, divaricately branched habit, small, glabrous leaves, capitate inflorescences with bright yellow and reddish petaloid involucre bracts, and flowers lacking petaloid scales (Figure 1). The specific epithet alludes to its characteristic habit. The species appears to have been first collected by J.P.H. Acocks in 1956, and has been consistently misidentified as *G. microphylla* (now *L. microphyllum*) since then.

We consulted the collections in BOL, NBG, PRE and SAM (acronyms after Holmgren *et al.* 1990) as these contain the most extensive holdings of the southern African winter rainfall flora, and studied the species in the field.

We also take this opportunity to provide new combinations for *Gnidia pedunculata* Beyers and *G. sericeocephala* (Meisn.) Gilg. ex Engl., which accord with *Lasiosiphon* in all critical morphological characters but lack combinations in this genus.

***Lasiosiphon rigidus* J.C.Manning & Boatwr., sp. nov.**

Resembling *Lasiosiphon microphyllum* (Meisn.) Meisn. and *L. polycephalus* (C.A.M.Mey.) H.Pearson in the involucre flower heads surrounded by petaloid bracts, but differing in the rigid, divaricately branched habit and five caducous involucre bracts, which are apiculate, yellow flushed with dark red and subglabrous or shortly sericeous with straight hairs; *L. microphyllum* has ascending branches, 5–8, obtuse, persistent involucre

bracts, which are yellow to green and densely pubescent with crisped hairs; *L. polycephalus* has a virgate habit and 3–6, obtuse, persistent involucre bracts, which are yellow or reddish brown and densely sericeous with broad, hairless margins.

**TYPE.**—South Africa, Northern Cape, 3219 (Wup-pertal): Tankwa [Tanqua] Karoo National Park, SW foot of Leeu-berg, along drainage lines. (–BB), 20 June 2012, Manning 3363 (NBG, holo.; K, MO, PRE, iso.).

Rigid, densely divaricately branched shrublet up to 0.6(–1.0) m high, branches suberect to spreading, sparsely leafy and glaucous when young but later developing grey, fissured bark. *Leaves* alternate, suberect or  $\pm$  spreading, rather distant, shortly petiolate, blade obovate to oblanceolate, 5–10(–12)  $\times$  (1.5–)2.0–4.0 mm, obtuse to acute, plane or shallowly concave, leathery, glaucous, midrib weakly raised beneath, petiole 0.2–0.5 mm long. *Inflorescence* terminal on main and lateral branches, capitate, bracteate,  $\pm 15$ –30-flowered, branches becoming hard and thorny with age; involucre bracts 5, ovate, 10–11  $\times$  5–6 mm, yellow  $\pm$  flushed wine-red or entirely maroon, papery, faintly nervate, apiculate, subglabrous to densely sericeous, caducous and mostly fallen at flowering. *Flowers* chrome-yellow with maroon tube, unscented during day but strongly lilac-scented at night; pedicel  $\pm 1$  mm long, densely appressed pubescent; hypanthium 13–18 mm long, circumscissile 4.5–6.0 mm from base, basal portion narrowly ovoid, densely sericeous with long, ascending, silvery to golden hairs 2–5 mm long, upper portion tubular but inflated and subglobular in distal 1.5 mm, densely appressed pubescent with straight, sericeous hairs  $\pm 1$  mm long in lower portion but becoming villous with crisped hairs distally, especially on distal swelling; sepals 5, spreading, ovate, 4–5  $\times$  2.0–2.5 mm, glabrous and waxy above but villous beneath, margins revolute and apex reflexed, thus apparently oblong-emarginate and  $\pm 1.5$  mm wide. *Petaloid scales* 0. *Stamens* 4 + 4, subsessile; outer whorl inserted 0.5 mm below rim of hypanthium, half-exserted; inner whorl inserted at base of bulge  $\pm 1.5$  mm within throat of hypanthium, fully included; anthers  $\pm 1$  mm long at anthesis. *Ovary* ellipsoid and attenuate basally,  $\pm 2$  mm long, sparsely sericeous; style inserted laterally, included and reaching less than halfway up hypanthium,  $\pm 4.5$  mm long, stigma penicillate. *Fruit* not seen. *Flowering time*: June–Sept. Figures 1, 2.

**Distribution and ecology:** evidently endemic to the central and eastern parts of the Tankwa Karoo, an arid basin between the Cedarberg and Roggeveld Mtns (Figure 3); the species is best known from around the Elandsberg, especially along the SW foot of the Leeu-berg. It is restricted to loamy soils on the banks and margins of seasonal washes and drainage lines and is never abundant. Plants are typically found growing through other, often strongly thorny or prickly shrubs.

*Lasiosiphon rigidus* is one of several shrubby species marking seasonal drainages in the Tankwa, others being *Osteospermum sinuatum* (DC.) Norl., *Berkheya spinosa* (L.f.) Druce, *Eriocephalus microphyllus* DC. and *Pteronia villosa* L.f. (all Asteraceae), *Aridaria noctiflora* (L.) Schwantes (Aizoaceae), and *Melolobium candicans* (E.Mey.) Eckl. & Zeyh. (Fabaceae).

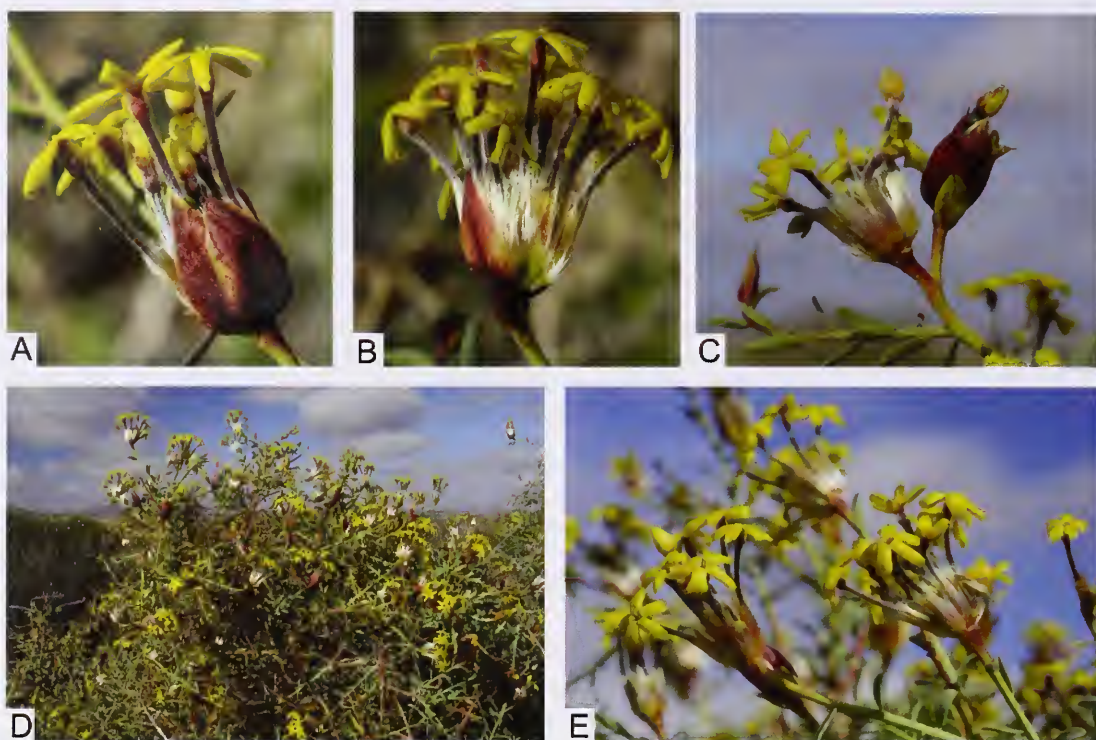


FIGURE 1.—Morphology and habit of *Laiosiphon rigidus*. A–C, E, inflorescences with flowers at various stages; D, rigid, divaricately branched shrubby habit. Photographs: John Manning.

**Diagnosis and relationships:** although initially confused with *Laiosiphon microphyllus*, a microphyllous subshrub from drier interior South Africa with similar involucre flower heads surrounded by petaloid bracts, *L. rigidus* is distinguished by its very different growth form and by the shape and vestiture of the involucre. *L. microphyllus* is a low-growing subshrub producing slender ascending stems with  $\pm$  appressed leaves, and virgate flowering branches 0.5–0.8 mm in diameter and leafy to the tips, with the uppermost leaves grading into 5–8 involucre bracts. The bracts persist through the flowering period and are obtuse and densely pubescent with crisped hairs. From herbarium specimens they appear to be pale yellow or greenish in colour. *L. rigidus* is a rigid, divaricately branched shrub with suberect or  $\pm$  spreading leaves and short flowering branches 1.0–1.5 mm in diameter, with the uppermost leaves distant and well differentiated from the strictly five involucre bracts. These are apiculate and subglabrous or shortly sericeous with straight hairs. The yellow bracts are almost completely flushed with dark wine red and are caducous, abscising soon after anthesis so that the flowers are left exposed. Although *L. microphyllus* is described as having small petaloid glands (Wright 1915), all the specimens that we have examined lack these glands.

*Laiosiphon rigidus* is evidently also allied to *L. polyccephalus* (C.A.Mey.) H.Pearson, a virgate subshrub widespread through the drier parts of the subregion, with similar scanty foliage and flowers in heads surrounded by yellow to reddish brown petaloid involucre bracts and lacking petaloid scales. It is recognised by its wiry,

well-branched stems with sharply ascending branches and numerous, small flower heads with less than ten flowers, subtended by densely sericeous bracts that are characterised by their broad, hairless margins. These three species all share densely sericeous fruits with very long hairs and appear to comprise a group of closely allied taxa from the arid South African interior.

#### Additional specimens seen

**NORTHERN CAPE.**—**3119** (Calvinia): Klipbank, SW of Calvinia on lower N slopes, (–DD), 23 July 1956, *Acocks 18870* (PRE). **3219** (Wuppertal): Tankwa Karoo National Park, Biesiesfontein, (–BB), 22 July 2006, *Manning 3014* (NBG); Tankwa Karoo National Park, foot of Leeueberg, (–BB), 3 Aug. 2006, *Sachse 48* (PRE); Tankwa Karoo National Park, N end of Leeueberg, E of Varsfontein, (–BB), 16 Aug. 2007, *Helme 4710* (NBG); Doornrivierkruising met Ceres, Sutherland pad, (–BC), 9 Jul. 1991, *Van Zyl 4198* (NBG); Tankwa Karoo National Park, Grasberg South 1103, (–BC), 16 Aug. 2008, *Steyn 1446* (PRE); Tankwa Karoo National Park, track to Volmoersfontein, S of Potkleiberg, (–BD), 6 Aug. 2009, *Steyn 1525* (PRE); Tankwa Karoo National Park, track between Luiperdskop and Varsfontein, (–BD), 15 Aug. 2011, *Steyn 1862* (PRE). **3220** (Sutherland): Tankwa Karoo National Park, Farm Leeukloof 114, slope W of Leeukloof, (–AC), Sept. 2007, *Sachse 618* (PRE).

**WESTERN CAPE.**—**3219** (Wuppertal): Farm Koffiewater, (–BC), 4 Aug. 2007, *Bester 7722* (PRE); **3220** (Sutherland): Tankwa Karoo National Park, near Paulshoek, (–AC), 27 Aug. 2004, *Steyn 624* (PRE); Bantamsfontein Kop (–CC), 17 June 1965, *Acocks 23667* (PRE).

Imprecise locality: Ceres Karoo, 13 May 1946, *Nel s.n. STE26832* (NBG, 3 sheets).

#### New combinations

With the reinstatement of the genus *Laiosiphon* by Beaumont *et al.* (2009), it is necessary to provide combi-



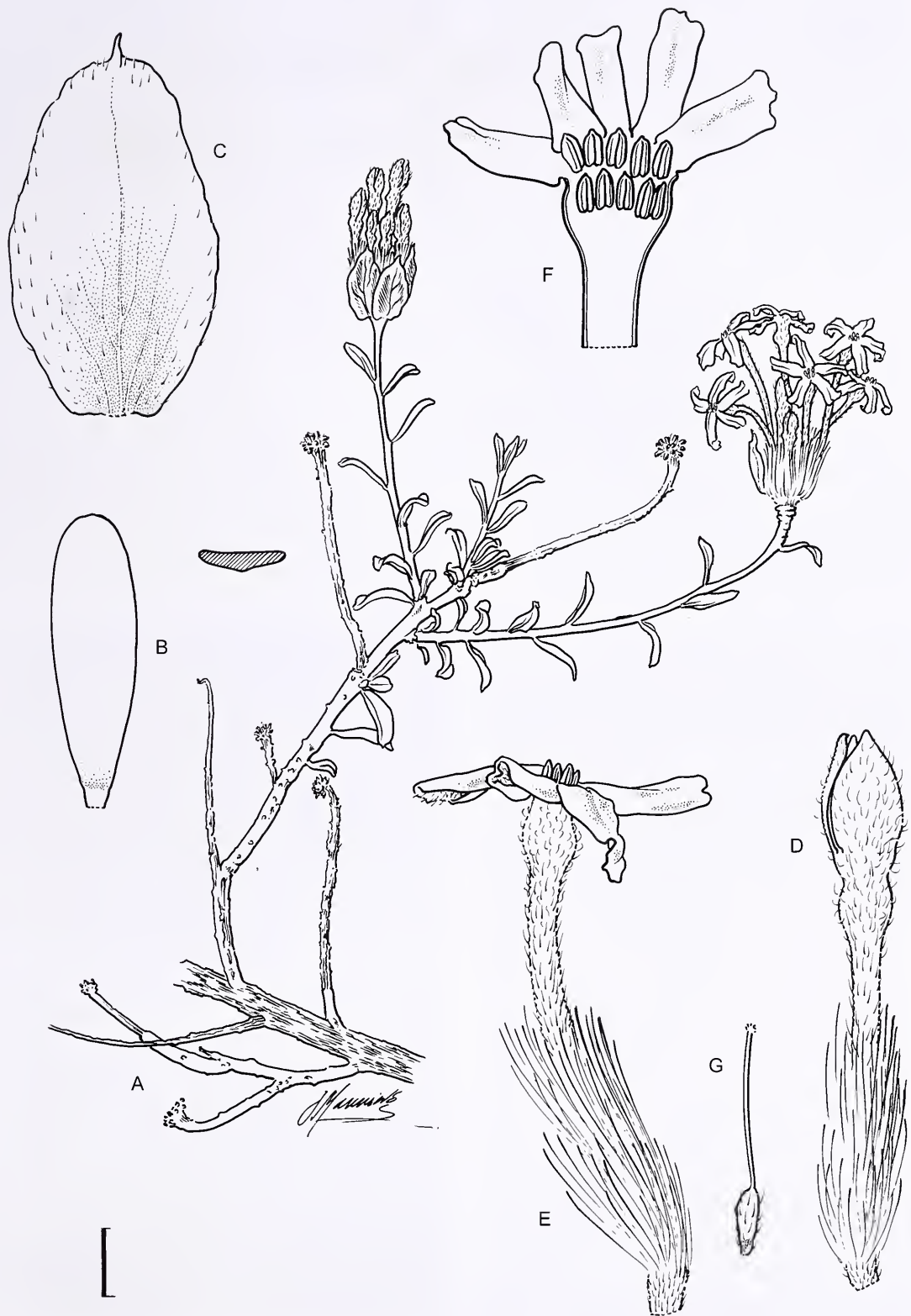


FIGURE 2.—*Laiosiphon rigidus*, Manning 3363. A, flowering branch; B, leaf and leaf T/S; C, involucral bract; D, bud; E, flower; F, open flower with detail of androecium; G, gynoecium. Scale bar: A, 10 mm; B–G, 2 mm. Artist: John Manning.



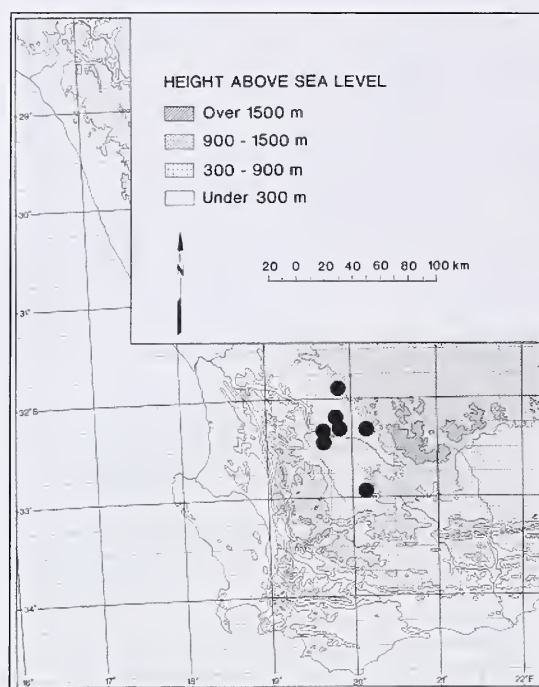


FIGURE 3.—Distribution of *Laiosiphon rigidus*.

nations for the following two species.

*Gnidia pedunculata* is a narrow endemic of the Knersvlakte resembling the group of three species of *Laiosiphon* discussed above in its glabrous stems and leaves and  $\pm$  capitate inflorescences with petaloid involucre bracts and waxy, golden yellow flowers with a pubescent hypanthium. It differs from them in its tetramerous flowers with small petaloid scales.

*Gnidia sericocephala* was one of 11 species treated by Wright (1915) in the genus *Arthrosolen* C.A.Mey., which was distinguished from *Gnidia* by the absence of petaloid scales. This character is now known to be variable within both *Gnidia* and *Laiosiphon*, and *Arthrosolen* was treated as a synonym of *Gnidia* by Peterson (1959, 1978). The three species with pentamerous flowers should, however, be included in *Laiosiphon*. Combinations in *Laiosiphon* exist for two of the species, viz. *L. polycephalus* (C.A.Mey.) H.Pearson and *L. calocephalus* (C.A.Mey.) Domke, but not for the third, *Gnidia sericocephala*.

***Laiosiphon pedunculatus* (Beyers) J.C.Manning & Boatwr., comb. nov.** *Gnidia pedunculata* Beyers in *Bothalia* 32: 79 (2002). Type: South Africa, Western Cape, 3118 (Vanrhynsdorp): Knersvlakte, Olifants River Settlement 316, near Eastern border, (–BC), 6 Aug.

1993, *Le Roux & Hilton-Taylor* 27 (NBG, holo.!; K, PRE, iso.).

***Laiosiphon sericocephalus* (Meisn.) J.C.Manning & Boatwr., comb. nov.** *Arthrosolen sericocephalus* Meisn. in DC., *Prodromus systematis naturalis regni vegetabilis* 14, 2: 561 (1857). *Gnidia sericocephala* (Meisn.) Gilg. ex Engl.: 634 (1921). Type: South Africa, 'In mont. Macalisberg Caffrariae', *Zeyher* 1494 (G-DC, holo.).

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SAPINDACEAE

ZANHA AFRICANA, A NEW DISTRIBUTION RECORD FOR NAMIBIA

*Zanha africana* (Radlk.) Exell is a tropical African savanna tree with a distribution that extends from Kenya southwards through Tanzania, Malawi, Mozambique, Zambia, Zimbabwe and southern Angola (Exell 1966; Beentje 1994) to Botswana (Archer 2003). In the *Flora of southern Africa* [FSA] region, *Z. africana* has hitherto only been recorded and mapped for the far northeastern corner of Botswana (Archer 2003; Van Wyk *et al.* 2011), though not taken up in Setshogo & Venter (2003).

In November 2009, the author undertook an expedition to the botanically poorly explored mountainous area on the southern side of the Kunene River in the Kaokoveld of northwestern Namibia. The focus was a survey of the species of *Euphorbia* between Ruacana and Swartbooisdrif. Near Okauapehuri, about 15 km to the south of the Kunene River, a strange tree with paripinnate leaves and velvety orange fruit was noted. Material was collected and subsequently positively identified as *Zanha africana* (Figures 1A, B; 2). The mature leaves (at least principal veins below, or rachis towards the base) and fruit are hairy to velvety in *Z. africana*, but

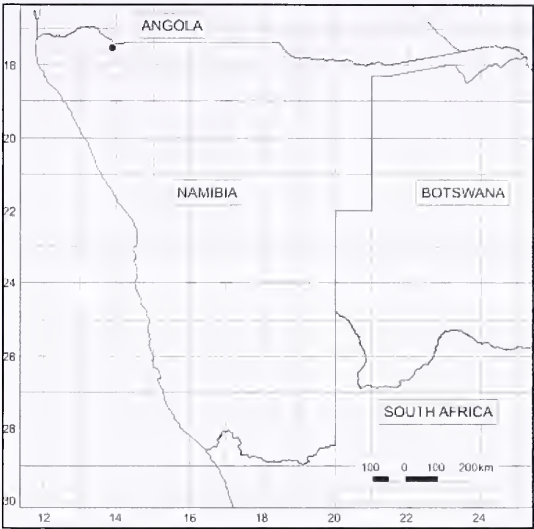


FIGURE 2.—Known distribution of *Zanha africana* in Namibia.



FIGURE 1.—*Zanha africana* in the Kaokoveld, Namibia. A, growth form, with tree  $\pm$  6 m high; B, twig with leaves and fruit ( $\pm$  25  $\times$  20 mm in diameter).

hairless in *Z. golungensis* Hiern, the only other member of the genus in southern Africa (Exell 1966; Coates Palgrave 2002). The Okauapehuri plants were bearing fruit in November, which corresponds to the season (November to January) given for *Z. africana* in Zimbabwe (Coates Palgrave 2002).

Despite a thorough survey of the area, only two plants were found. These were growing close to each other on a north-facing aspect of a wooded east–west orientated low hill at an altitude of 1 400 m. Both were medium-sized trees of  $\pm$  6 m high and in fruit. It is suggested that environmental factors in Namibia are marginal for the species. The hot and relatively arid conditions of the Kaokoveld habitat are most probably responsible for the smaller size and rarity of specimens in this part of its range. Elsewhere in Africa *Zanha africana* is reported as being a tree up to 10 m high or a shrub occurring in woodland, often on granite ridges or kopjes and occasionally in riverine forest (Exell 1966). When shown to the local Ovahimba inhabitants, it was mentioned to the author that the tree is unknown to them. In fact, they wanted to know from the author whether the fruit were edible or not.

The two plants mentioned above represent the first record of *Zanha africana* for Namibia (Figure 2), a range extension of  $\pm$  1 250 km to the west of the nearest hitherto known localities for the FSA region in north-eastern Botswana. Figueiredo & Smith (2008) do not mention this species in their comprehensive floristic inventory for Angola but, following Exell & Mendonça (1954), only *Z. golungensis* Hiern. The two syntypes of *Z. golungensis* (Welwitsch 4545, 4546) are from the Cuanza Norte Province in Angola (Hiern 1896). Con-



sidering the reported presence of *Z. africana* in southern Angola (Exell 1966), and its subsequent mapping for this region (Lebrun & Stork 2011), the Namibian plants of this species are almost certainly a cross-border outlier of the populations in nearby Angola. This suggests that both *Z. africana* and *Z. golumgensis* are present in Angola, as is mapped by Lebrun & Stork (2011). According to Exell (1966), the two species are sometimes difficult to separate in the absence of flowers or fruit and where their distribution overlaps. However, whether these two species indeed deserve separate distinction at species level requires further study.

#### Key specimen examined

NAMIBIA.—1713 (Swartbooisdrif): Okauapehuri, N-facing slope of hill to the S of settlement (–DB), 29 Nov. 2009, Swanepoel 294 (WIND, PRE).

*Additional specimens* [<sup>(1)</sup> = *Z. africana*; <sup>(2)</sup> = *Z. golumgensis*]

*Aguilar Macedo* 2755 <sup>(1)</sup> (PRE) [MOZAMBIQUE]; *Angus* 1786 <sup>(1)</sup> (PRE) [ZAMBIA]; *Banda & Kaunda* 3630 <sup>(1)</sup> (PRE) [MALAWI]; *Blomberg et al.* 437 <sup>(1)</sup> (PRE, photostat) [BOTSWANA]; *Chase* 272 <sup>(2)</sup> (PRE) [ZIMBABWE]; *Chase* 8341 <sup>(2)</sup> (PRE) [ZIMBABWE]; *Chase* 950 <sup>(1)</sup> (PRE) [ZIMBABWE]; *De Winter* 9416 <sup>(1)</sup> (PRE) [ZIMBABWE]; *Gereau & Congdon* 2475 <sup>(1)</sup> (PRE) [TANZANIA]; *Goldsmith* 27/62 <sup>(2)</sup> (PRE) [ZIMBABWE]; *Gomes Pedro* 4390 <sup>(2)</sup> (PRE) [MOZAMBIQUE]; *Greenway & Kirrika* 11068 <sup>(2)</sup> (PRE) [TANZANIA]; *Jacobson* 2944 <sup>(1)</sup> (PRE) [ZIMBABWE]; *Lovemore* 334 <sup>(1)</sup> (PRE) [ZIMBABWE]; *Macuacua* 1419 <sup>(1)</sup> (PRE) [MOZAMBIQUE]; *Merello et al.* 1950 <sup>(2)</sup> (PRE) [ZAMBIA]; *Milne-Redhead* 3700 <sup>(1)</sup> (PRE) [ZAMBIA]; *Milne-Redhead* 4467 <sup>(1)</sup> (PRE) [ZIMBABWE]; *Texeira et al.* 9455 <sup>(2)</sup> (PRE) [ANGOLA]; *Torre & Paiva* 9496 <sup>(1)</sup> (PRE) [MOZAMBIQUE]; *Willan* 595 <sup>(2)</sup> (PRE) [TANZANIA].

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#### ORCHIDACEAE

##### *HABENARIA AMOENA* NEWLY RECORDED FOR NAMIBIA

The orchid flora of Namibia is depauperate compared to the rest of sub-Saharan Africa, and only 17 species have so far been documented for the country (WCSP 2012). These include one species each of *Ansellia* Lindl., *Bartholina* R.Br., *Bonatea* Willd. and *Holothrix* Rich. ex Lindl., eight species of *Eulophia* R.Br. ex Lindl., and five species of *Habenaria* Willd. (WCSP 2012). Much of the country is arid and thus not suitable for orchids; whereas more humid parts, such as the Caprivi Strip, are underexplored.

In the course of 2010, an orchid specimen (*Mannheimer & Greeff* 4394, Figure 1) was sent to the author by the Windhoek Herbarium (WIND) for identification. On first impression it looked like the fairly common and widespread *Habenaria malacophylla* Rchb.f., which has not been recorded for Namibia. However, *H. malacophylla* is typically associated with upland,

closed-canopy rain forest, a habitat not found in Namibia.

A closer examination of the plant and keying it out in the Flora of Tropical East Africa (Summerhayes 1968) and Flora Zambesiaca (La Croix & Cribb 1995), revealed that it was a specimen of *Habenaria amoena* Summerh., previously only recorded from the Democratic Republic of the Congo, Tanzania, Malawi, Zambia and Zimbabwe. The morphological differences between *H. amoena* and *H. malacophylla* are subtle but clear (Table 1). The specimen itself closely matches the type of *H. amoena* (*Richards 1000* (K), sheet I and II) and the dissected flower matches the drawings made by Summerhayes (1968) and attached to the type as sheet III (all downloaded from JSTOR Plant Science).

The habitat of *H. amoena* has been reported as “open woodland and scrub” (Summerhayes 1968), “woodland,





FIGURE 1.—*Habenaria amoena*. A, plant in situ (photograph: Coleen Mannheimer); B, image of specimen: Mannheimer & Greeff 4394.

TABLE 1.—Vegetative and floral characters that distinguish *H. amoena* from *H. malacophylla*

Feature	<i>H. amoena</i>	<i>H. malacophylla</i>
Stem	Leafy along its entire length.	Only leafy in the centre and bare in the lower part.
Flowers	Nearly horizontal.	Curved outwards.
Lip	Decurved.	Projecting outwards.
	Base undivided for about 1.5 mm.	Trilobed nearly to the base.
	Side lobes considerably longer than midlobe.	Side lobes slightly longer than midlobe.
Spur	17–22 mm [19–20 mm in specimen].	9–18 mm.
	Only slightly swollen in apical half.	Thicker in the middle than at either end.
Anther	2 mm high.	1.5 mm high.

rocky hillsides” (La Croix & Cribb 1995) and “*Brachystegia* woodland” (La Croix *et al.* 1991), which is similar to the habitat where this particular specimen was collected from, namely “mixed bushveld”.

***Habenaria amoena* Summerh.** in Kew Bulletin 11: 218 (1956). Type: Zambia, Abercorn district, Chitlongowelo, *Richards 1000* (K, holo.—JSTOR plant Science image!).

*Specimen examined*

NAMIBIA.—1917 (Tsumeb): Otjozondjupa, Otavi , small holding near Otavi, 19° 38.853’S; 17° 21.975’E (–CB), 1 440 m, 13 Mar. 2009, *Mannheimer & Greeff 4394* (WIND).

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## ASTERACEAE

A NEW NAME AND NEOTYPIFICATION FOR *HIPPIA INTEGRIFOLIA* (ANTHEMIDEAE)

*Hippia integrifolia* Less. (1832), a name currently applied to a species endemic to the Langeberg mountains in the Cape Floristic Region of South Africa, is a later homonym of *Hippia integrifolia* L.f. (1782). The latter is a name previously and validly published for a widely distributed species, described by the younger Linnaeus from a specimen collected in India and currently placed within the genus *Dichrocephala*, as *D. integrifolia* (L.f.) Kuntze (Fayed 1979; Pruski 2011).

Although De Candolle (1838) clearly indicated Lessing's use of the name in a sense other than that proposed by Linnaeus, subsequent authors have overlooked the matter, attributing the name to Lessing (Harvey 1865; Hutchinson 1918; Merxmüller 1950; Bond & Goldblatt 1984; Goldblatt & Manning 2000; Germishuizen *et al.* 2006; Kloppe *et al.* 2006). As a result, no other available names for this taxon exist.

Lessing's species is clearly very closely related to another species, *H. trilobata* Hutch., which is also restricted to the Langeberg mountains. In fact, Merxmüller (1950) suggested that *H. trilobata* may be insufficiently distinct from *H. integrifolia* Less. on the grounds of leaf variation within both *H. integrifolia* Less. and the genus in general. Unfortunately, flowering and fruiting material of *H. trilobata* has only recently become available (Brusse 3590, NBG, PRE), so that neither Hutchinson (1918) nor Merxmüller (1950) were able to compare the fruit. We therefore studied the available fruit material of the two species from collections at BOL, NBG, PRE and SAM and came to the conclusion that they are certainly distinct. The fruit of Lessing's *Hippia integrifolia* have very broad membranous wings (Figure 1A), while those of *H. trilobata* are only very narrowly membrane-rimmed (Figure 1B). Although the leaves of Lessing's *H. integrifolia* may become apically two- or three-lobed in the uppermost portion of the flowering stems, they are predominantly entire (Figure 1D–F), unlike the smaller, consistently three-lobed leaves of *H. trilobata* (Figure 1C).

Lessing (1832) referred to a single collection in the protologue, viz. a specimen from the Cape of Good Hope in Vahl's herbarium ("v. sp. in hrb. Vahliano, in Prom. b. sp. lectum"). The only specimen that could be found in Vahl's herbarium, now housed in the Natural History Museum of Denmark (C), was that of Ecklon 317 (70.10). However, this specimen bears no annotation by Lessing nor is there any indication that he ever saw it. Elsewhere in his treatment, Lessing very clearly and unambiguously cites Ecklon material (i.e. for *Berkheya carlinoides* he lists "Ecklon in Zwellendamsi monte in et supra Voormansbosch Octbr."), so it seems reasonable to assume that had he been referring to Ecklon's collection of *H. integrifolia*, he would have similarly indicated it. Subsequent searches of the herbaria of the Botanical Museum Berlin-Dahlem (B) and the Swedish Museum of Natural History (S) also failed to uncover any original material.



FIGURE 1.—Fruit and leaves of *Hippia simplicior* (A, D–F) and *H. trilobata* (B, C). Vouchers: A, Du Plessis 76 (NBG); B, C, Brusse 3590 (NBG); D, E, F Helme 4629 (NBG). Scale bars: 1 mm.

As *H. integrifolia* Less. is an illegitimate name and so unavailable for use, a new name is provided here. Furthermore, we designate a neotype from the widely distributed Ecklon collection until such time as original elements can be definitely identified.

***Hippia simplicior* Magee & B. Busch nom. nov. pro *Hippia integrifolia* Less., Synopsis generum Compositarum: 268 (1832), hom. illegit. non L.f. (1781). Type: Western Cape, Swellendam, Oct., Ecklon 317 (SAM, neo! , here designated; C – photo!, G-DC, MO, S, TCD – photo! isoneo.).**

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## ASTERACEAE

TWO NEW COMBINATIONS IN *CAPUTIA* AND *CURIO* (SENECIONEAE)

Ongoing phylogenetic studies into generic delimitations in Senecioneae have resulted in the description or resurrection of a number of genera for segregates of the large genus *Senecio* L. (Nordenstam *et al.* 2009). Among those described for southern African species are the two genera *Caputia* B.Nord. & Pelser (2012) and *Curio* P.V.Heath (1997). Two recently discovered species described in *Senecio* belong in these genera, but lack the relevant combinations.

*Caputia* was described (Nordenstam & Pelser 2012) for a small group of species that is only distantly related to *Senecio* s. str. and possibly of hybrid origin (Pelser *et al.* 2007). This distinct assemblage of succulent species is characterised by its mostly tomentose foliage and large, radiate or discoid capitula. The genus currently includes four species distributed along the eastern coastal regions of southern Africa. A fifth species, *Senecio oribiensis* Van Jaarsv., allied to *C. medley-woodii* (Hutch.) B.Nord. & Pelser (= *S. medley-woodii* Hutch.), was recently described from Oribi Gorge in KwaZulu-Natal (Van Jaarsveld 2012) and requires a combination in the genus.

***Caputia oribiensis* (Van Jaarsv.) J.C.Manning**, comb. nov. *Senecio oribiensis* Van Jaarsv. in *Aloe* 48: 78 (2012). Type: South Africa, KwaZulu-Natal, Oribi Gorge, *Van Jaarsveld* 22763 (PRE, holo.).

*Curio* currently includes 20 species of mostly sprawling or prostrate succulents with  $\pm$  fusiform leaves and discoid capitula, distributed mostly through the drier parts of southern Africa. The recently described *Senecio pondoensis* Van Jaarsv. & A.E.van Wyk from the Mzamba River Gorge in Eastern Cape is another member of this group, allied to *C. talinoides* (DC.) P.V.Heath (1999) (= *S. talinoides* DC.), but as yet lacking a name in the genus *Curio*.

***Curio pondoensis* (Van Jaarsv. & A.E.van Wyk) J.C.Manning**, comb. nov. *Senecio pondoensis* Van Jaarsv. & A.E.van Wyk in *Aloe* 45: 28 (2011). Type: South Africa, Eastern Cape, Mzamba River Gorge, *Van Jaarsveld et al.* 19297 (PRE, holo.).

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## ASTERACEAE

*DISTEPHANUS* (ASTERACEAE: VERNONIEAE): A NEW COMBINATION AND A NEW RECORD FOR SOUTHERN AFRICA

The name *Distephanus* Cass. has been applied to species of Vernoniaceae with trinervate leaves, predominantly yellowish flowers (some are reddish or purplish), distinct basal stylar nodes, and sclerified basal appendages on the anther thecae. The genus occurs in Asia, the western Indian Ocean, Madagascar, and eastern Africa (Robinson & Kahn 1986). Although Robinson & Kahn (1986) recognised 26 species in *Distephanus*, they indicated that others probably belonged to it as well, anticipating the future addition of new species, and the most recent tribal treatment (Keeley & Robinson 2009: Table 28.1) estimated 50 species of *Distephanus*. Neither of these treatments suggested that *Vernonia inhacensis* G.V.Pope should be included in the genus, but it has the defining morphological features for *Distephanus*. Robinson & Kahn (1986) stated that a distinct puck-like node at the base of the style is 'almost totally restricted to and characteristic of *Distephanus* among the paleotropical Vernoniaceae' and also pointed out the simple broad sclerified shield of the anther endothecium. Both of these features, as well as the trinervate leaves are present on plants of *V. inhacensis*. We transfer *V. inhacensis* to the genus *Distephanus* and distinguish it from *D. divaricatus* (Steetz) H. Rob. & B. Kahn and *D. anisochaetoides* (Sond.) H. Rob. & B. Kahn.

***Distephanus inhacensis*** (G.V.Pope) Boon & Glen, comb. nov. *Vernonia inhacensis* G.V.Pope in Kew Bull. 43: 280 (1988); G.V. Pope in Flora zambesiaca 6: 81 (1992). Type: Mozambique, Xai-Xai, Praia Sepulveda, Barbosa & Lemos 7843 (K—ALUKA image!, holo.; COI—ALUKA image!, LISC—ALUKA image!, iso.).

[*Distephanus* sp. nov. Boon: 584 (2010)]

**Distribution and ecology:** known from just north of the Tongati River at the Zimbali Estate to southern Mozambique near Xai Xai. Pope (1988) describes the distribution as 'Mozambique, South Africa (Natal and Zululand)' but subsequently (Pope 1992) states that the species is 'not known from outside the Flora Zambesiaca area'. The species is a component of dune scrub thickets and forest and coastal woodlands. Flowering is (July–)Aug.–Oct.(–Nov.).

**Common name:** a suggested English name is coastal bitter-tea.

**Discussion:** South African material of *D. inhacensis* has often been misidentified as *D. divaricatus* (= *Vernonia aurantiaca* (O.Hoffm.) N.E.Br.) (Hilliard 1977). In the FSA Region, *D. divaricatus* is restricted to Mpumalanga, Limpopo Province, Namibia and Botswana, while *V. inhacensis* has an eastern coastal distribution in KwaZulu-Natal and southern Mozambique (Figure 1). Although Hilliard (1994) recognized *V. inhacensis* as a separate species in these coastal areas, the species remained poorly understood and was treated as *Distephanus* sp. nov. (Boon 2010). *Vernonia inhacensis* can easily be distinguished from *D. divaricatus* by its con-

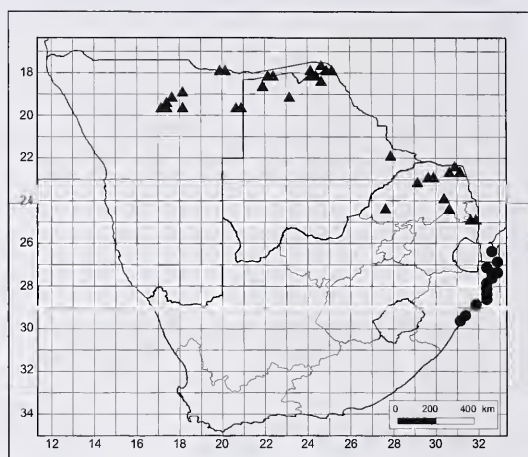


FIGURE 1.—Distribution of ●, *Distephanus inhacensis* and ▲, *D. divaricatus* in southern Africa based on specimens at NU, CPF, NH, PRE.

colourous leaves and white to cream flowers with yellow anthers whilst *D. divaricatus* has leaves that are pale grey to whitish below, and orange-yellow flowers. *D. divaricatus* also has a conspicuous tuft of white hairs at the base of the petiole, which is absent in *V. inhacensis*. Specimens of *V. inhacensis* from southern Mozambique were reported by Pope (1992) to have purplish flowers, as was the collection of Ngwenya 2458, but Hilliard (1994) was of the opinion that these descriptions were in error and that the species had only white to cream-coloured flowers. We have not seen any purplish flowers among those observed in the field nor is that colour mentioned on any herbarium sheet examined besides Ngwenya 2458. Interestingly, two of the five southern African species, the subject of this note and *D. anisochaetoides* have white flowers, a colour not mentioned by Robinson & Kahn (1986) and Keeley & Robinson (2009).

*Distephanus inhacensis* is a liana growing to about 8 m and the deeply furrowed stems reach about 120 mm in diameter (Figure 2A). *D. divaricatus* also grows to about 8 m, but is a shrub or climber. Leaves, inflorescences and young stems usually have scattered short, whitish to brown hairs in *V. inhacensis*, whilst in *D. divaricatus* young branches are whitish tomentellous or puberulous to glabrescent (Pope 1992). In *V. inhacensis* leaves are alternate, ovate(elliptic), green above and below, trinerved, entire and usually mucronate (Figures 2A, B, C). They reach  $\pm 60 \times 35$  mm (*D. divaricatus* has leaves reaching  $120 \times 100$  mm) and may be slightly succulent and glabrous when growing on coastal dunes; more inland they tend to be thinner and hairier. Inflorescences are terminal and sub-terminal panicles, and immature heads may persist for some weeks along the branches of the inflorescences before opening to flower (Figure 2A,

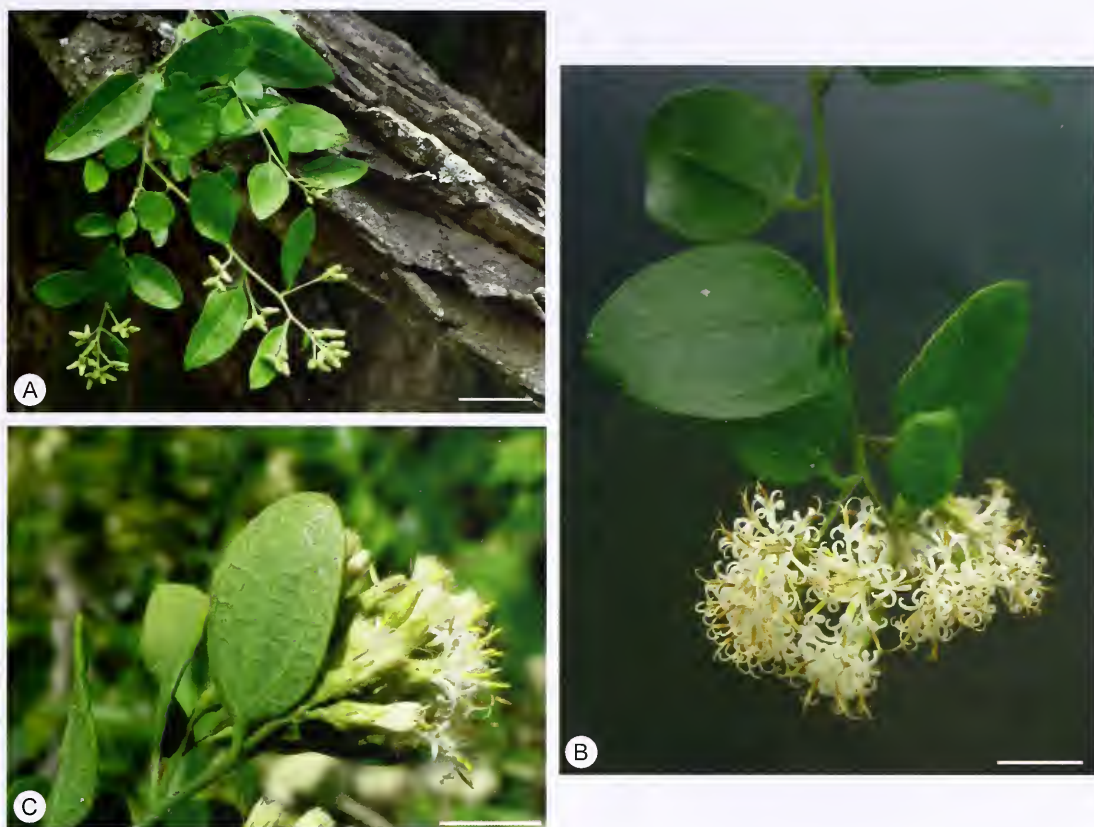


FIGURE 2.—*Distephanus inhaensis*. A, branchlet with inflorescence in bud. Large stem with a diameter of approximately 100 mm in the background; B, flowering branchlet; C, flowering branchlet showing succulent leaves with three prominent nerves (abaxial view). Note vestiture on branches and petioles. Photographs: Richard Boon. Scale bars A, 30 mm; B,C, 10 mm.

B, C). The cypselas are sparsely hispidulous with a pappus of both scales and setae. In *D. divaricatus* the cypselas are densely strigose and the pappus is composed of scale-like setae (Pope 1992). Additional characters of both species are described by Pope (1992).

Although *D. inhaensis* has been most often confused with *D. divaricatus*, another species, *D. anisochaetoides*, is the most similar South African species, with similar habit and white to cream flowers. *D. anisochaetoides* is distinguished from *D. inhaensis* by its larger,  $\pm 85 \times 70$  mm, slightly discoloured and broadly ovate to cuneate-rhomboid leaves with cuneate bases and usually coarsely toothed margins, especially on the upper half. It has larger capitula, with  $\pm 15$ –20 florets per capitulum versus  $\pm 9$  in *D. inhaensis*. Additionally, *D. anisochaetoides* has a generally more temperate distribution in coastal, scarp and mistbelt forest margins from the Eastern Cape to Mozambique, although the two species may grow side-by-side in coastal forests and thickets. Additional characters of *D. anisochaetoides* and *V. inhaensis* are described by Pope (1992).

**Conservation status:** *D. inhaensis* is both quite common and fairly widespread, and so should be listed as being of Least Concern (*sensu* Raimondo *et al.* 2009) throughout its range.

#### Additional specimens

KWAZULU-NATAL.—**2732** (Ubombo): Sihangwane, (–AD), 14 Sept. 1973, *E.S. Pooley 1664* (NU); Mazengwenya, dune bush, (–BB), 11 Sept. 1971, *R.G. Srey 10454* (PRE); Lake Sibaya, Camp Abandon, (–BC), 4 Sept. 1996, *I. Felton and M. Thornhill 143* (PRE); Kosi Bay Coastal Forest Reserve, Lake Sibaya, eastern side along road between lake and first dune, forest, (–BC), 24 Aug. 1994, *R.A. Lubbe 253* (NH); Mazengwenya Coastal Forest, (–BD), 25 Feb. 1982, *E. Retief 851* (PRE); Mazengwenya, margin of dune forest, (–BD), 17 Aug. 1985, *M.C. Ward 1009* (NH, PRE); Mazengwenya Coastal Forest, (–BD), 25 Feb. 1982, *E. Retief 851* (PRE); Hlabisa District, False Bay, in bush at edge of bay, (–CD), 14 Sept. 1953, *Ward 1473* (NH); Sodwana Bay, (–DA), 05 Sept. 1982, *J.P. Kluge 2529* (PRE); Road to Sodwana Bay, (–DA), 29 Aug. 1978, *L. Smook 1306* (PRE); Sodwana Bay, forest, (–DA), 17 Sept. 1965, *J. Vahrmeijer 1157* (NH, PRE). **2831** (Nkandla): Mtunzini, (–DD), 14 Oct. 1973, *O.M. Hilliard & B.L. Burt 6845* (NU); Mtunzini, (–DD), *J. Gerstner* (NH); Mtunzini dunes, (–DD), 30 Sept. 1951, *G.S. Lawn 2131* (NH). **2832** (Mtubatuba): Eastern Shores State Forest, developing dune woodland, (–AB), 31 July 1985, *D.R. MacDevette 834* (NH); Nyalazi State Forest, Kentron area, in forest canopy, (–AB), 10 Sept. 1986, *G.F. van Wyk 914* (CPF, NH); St Lucia, Eastern Shores, Perriers Rocks forestry hut, seaward facing dune thicket, (–AB), Sept. 1982, *D.R. MacDevette 253* (NH); St Lucia, False Bay, (–AD), 26 Aug. 1978, *Johannesburg Botanical Garden 1781* (PRE); Eastern Shores State Forest, foredune at Perriers, dune forest, (–AD), 23 July 1986, *K. MacDevette 1007* (CPF); Dukuduku State Forest, Transect E, in forest, (–AD), 3 Sept. 1986, *K. MacDevette 1054* (CPF, NH); Mapelane, margin of dune forest, (–AD), 24 Sept. 1971, *C.J. Ward 7214* (NU, PRE); Lake Nhalabane area, South Lake, southern shores, dune woodland, (–CB), 05 Jan. 1992, *C.J. Ward & A. Rajih 11705* (NH); Futululu, Dukuduku, forest scrub, (–CC), 9 Sept. 1971, *R.G. Srey 10412* (PRE); Umhlatuzi Lake Bluff, in forest patch on dunes, (–CC), 11 July 1967, *H.J.T. Venter 3851* (PRE). **2931**



(Stanger): Mvoti River mouth, (–AD), 14 Oct. 1965, *E.J. Moll* 2568 (NU, PRE); Gingindhlovu, (–BA), Sept. 1932, *J. Gerstner* (NH); Balitoville, Zimbali dune forest, scrambling over foredune scrub, (–CA), 5 Sept. 1985, *K. MacDevette* 317 (NH, PRE).

MOZAMBIQUE.—2632 (Bela Vista): Ponta Milibangalala, (–BC), 29 Nov. 2001, *A.M. Ngwenya* 2458 (NH).

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## Notes on naturalised plants

VARIOUS AUTHORS

### *PETIVERIA ALLIACEA* IN KWAZULU-NATAL, SOUTH AFRICA

*Petiveria alliacea* L. is a New World herbaceous perennial of the family Phytolaccaceae. It has a wide natural distribution from Texas and Florida in the southern United States (Patton & Judd 1986; NatureServe 2011) southward to Ecuador (Jørgensen & León-Yáñez 1999) and Argentina (USDA 2011) as well as on a number of Caribbean islands (Zanoni & Buck 1999; USDA 2011). It is commonly known as Guinea-hen weed, *erva-Guiné* or *anamú* (Spanish) or *mucura caa* (Portuguese) (Defilips & Maina 2002; Glen 2004; Nienaber & Thieret 2008). The generic name honours James Petiver (1658–1718), an English apothecary and botanist (Nienaber & Thieret 2008). The specific epithet *alliacea* refers to the garlic odour emitted from its crushed leaves (Hecklau *et al.* 2005). *Petiveria alliacea* does not tolerate frost (Lonard & Judd 1991) and in its native range occurs in coastal regions, evergreen or deciduous woodland, secondary thickets as well as pastures and shrublands (Vázquez & Kolterman 1998; Jørgensen & León-Yáñez 1999).

*Petiveria alliacea* is cultivated as an ornamental garden plant in South Africa (Glen 2004), the earliest recorded collection dating back to 1883 (Wood 415, NH) from the Durban Botanical Gardens. In 1932 and 1979 further collections were made from cultivated plants in the gardens (Anon. s.n., NH; Du Toit 2749, NH; Pienaar 74, NH). In 1980, another cultivated specimen was collected from the ‘Durban Botanical Research Unit’ (Du Toit 2782, NH), which is an older name for the KwaZulu-Natal Herbarium. *Petiveria alliacea* is not represented at Compton Herbarium and the National Herbarium only has a cultivated specimen that is a duplicate of one of the KwaZulu-Natal specimens.

The first collection from non-cultivated plants in South Africa was made in 1989 (Ngwenya 571, NH) on the KwaZulu-Natal herbarium grounds. Currently, the plant is common on the herbarium grounds (Cheek 928, NH) despite not being actively cultivated. In a survey in August 2011, plants were found in two main clumps—671 individuals close to the herbarium and 198 in the northern corner of the botanical gardens (Figure 1). Thus far it has not been found in surveys of gardens or natural vegetation.

In January 2012, 500 plants were also found in the gardens of a neighbouring block of flats. All plants have since been cleared (by the botanic gardens authorities and the management of the flat-block respectively). This species could be classified at the D2 stage of invasion according the scheme proposed by Blackburn *et al.* (2011) because it has established self-sustaining, reproducing populations a significant distance from the point of introduction.



FIGURE 1.—Known distribution of naturalised *Petiveria alliacea* in KwaZulu-Natal, South Africa.

Introduced plants can be considered naturalised when self-sustaining populations persist for at least 10 years without direct human intervention, by recruitment from seed or ramets (Pysek *et al.* 2004). The current paper is the first record of naturalisation for *Petiveria alliacea* in South Africa. However, it has been recorded as naturalised in forest edges and disturbed sites in Benin and Nigeria and also in India (Schmelzer & Gurib-Fakim 2008). Although the Flora of West Tropical Africa (Hutchinson & Dalziel 1928) makes no mention of the plant, Olaifa *et al.* (1987) recorded it as indigenous to Nigeria, suggesting naturalisation occurred in the middle of the twentieth century. It is listed in the Global Compendium of Weeds (Randall 2007). In a survey of parks, gardens and abandoned areas of Curitiba (Brazil), Biondi & Pedrosa-Macedo (2008) recorded it as alien to the region but not displaying serious invasive characteristics.

In Durban, flowering starts in spring and ends in autumn when the racemes of white flowers are replaced by small compact achenes. Forty of the plants counted in August 2011 had fruit and none were flowering. The infructescence resembles that of *Achyranthes* L. spp.



FIGURE 2.—*Petiveria alliacea* L. A,B, flowers; C, inflorescence; D, fruits; E, habit; F, young plant. Photographs: M. Cheek.



(Amaranthaceae) and the dispersal method is the same, namely sticking to clothes or fur (epizoochory; Mori & Brown 1998). Each fruit is armed with four 'hooks' at the apex, which are effective in adhering to clothing. In an investigation into the dispersal ability using clothes Bullock & Primack (1977) found mean dispersal distances of 107 m in forest understory vegetation for *P. alliacea* and a mean distance of 33 m along roadside vegetation. In addition, the fruit can be wind dispersed (Schmelzer & Gurib-Fakim 2008). This plant could also become problematic for agriculture as it taints cattle milk with a garlic smell and has been reported to cause nitrate poisoning in cattle if browsed regularly (Schmelzer & Gurib-Fakim 2008; Nienaber & Thieret 2008).

The family Phytolaccaceae contains a number of well-known South African weeds: *Phytolacca octandra* L., *P. dioica* L., *P. americana* L. and *Rivina humilis* L. The belhambra tree, *Phytolacca dioica*, is a category 3 plant under the Conservation of Agricultural Resources Act and *Rivina humilis*, the blood berry, is a proposed category 1a plant under the National Environmental Management: Biodiversity Act (Act No. 10 of 2004).

As such, given the observed tendency to spread, its invasiveness in other countries, and related species being invasive, we would recommend that the species is placed on the species-under-surveillance list, and that further studies are conducted to assess whether it should be included in invasive species regulation. Publicity material requesting sightings of *Petiveria alliacea* will be distributed with a request for sightings to be sent to alienplants@sanbi.org.za.

2371.000 *Petiveria alliacea* L., Species plantarum 1: 342 (1753). Type: *Clifford 141* (BM, lecto. —JSTOR Plant Science image!, website accessed 04-10-2012). [For complete synonymy see Marchioretto (1989).]

Perennial, multi-stemmed, herb or woody shrub, up to 2 m tall. *Stems* round to terete, glabrous or faintly hairy, red when young, turning green, up to 12 mm diam. *Bark* lenticillate, green turning grey-white with age. *Stipules* paired, linear, persistent on lower stems after leaves have dropped, 1.5–2.0 mm long. *Leaves* simple, alternate, glabrous above and below, sometimes sparingly puberulent on abaxial veins, soft, green, margin entire, petiolate, ovate to oblanceolate, up to 200 × 72 mm, base attenuate, apex acute, acuminate or obtuse; petioles up to 10 mm long. *Inflorescence*: branched, dense racemes, up to 450 mm long, terminal or axillary; bracts lanceolate to deltate, 1–3 mm long, bracteole 1 mm long. *Receptacle* with sepals green with white margins, 5 × 2 mm. *Flowers* with tepals white or pink, up to 6 × 1 mm, reflexed, linear to oblong, prominently 3- to 5-veined, anthers exerted. *Achenes* up to 12 × 3 mm, green turning white with age, appressed to the infructescence axis and with 4 retrorse awns at the apex, peduncles to 2 mm. Flowering time in South Africa: spring to autumn. Figure 2.

#### Specimens examined

KWAZULU-NATAL.—2931 (Stanger): Durban Botanic Gardens, (—CC), Mar. 1932, *Anon. s.n.* (NH); 20 Apr. 1979, *P.C.V. du Toit* 2749

(NH); 12 Mar. 1979, *B. J. Pienaar* 74 (NH); Jan. 1883, *J.M. Wood* 415 (NH); Durban, KwaZulu-Natal herbarium grounds, 22 July 2011, *M. Cheek* 928 (NH); 29 Jan. 1980, *P.C.V. du Toit* 2782 (NH); 17 Feb. 1989, *A.M. Ngwenya* 571 (NH).

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# FSA contributions 21: Connaraceae

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**Keywords:** Connaraceae, Fabaceae, heterostyly, Oxalidales, southern Africa, taxonomy

## INTRODUCTION

Connaraceae R.Br. comprise mostly woody climbers, which climb by means of the winding ends of young branches, less often shrubs or small trees, and rarely rhizomatous shrublets. In the FSA-region, members are recognized by alternate, exstipulate, imparipinnately compound leaves, with transversely-ridged petioles; entire leaflet margins and oblique bases (*Cnestis*); and the actinomorphic, 5-merous flowers with stamens of two lengths. The usually single follicles are  $\pm$  ridged and swell to almost mature size well before the solitary, black or red arillated seeds develop, with the ripe seeds partly squeezed out of the follicle. Connaraceae are pan-tropical in distribution, but mainly southern hemisphere, with species occurring in both the Old and New World. Members of the family can be found in lowland rain forest or forest patches in savannas (Heywood 2007).

Cronquist (1981) placed Connaraceae in the Rosales and Takhtajan (1997) in the Connarales. The APG II and APG III (2003, 2009) and Reveal (2012) place the family in order Oxalidales, next to the Oxalidaceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, and Elaeocarpaceae. Phylogenetic studies showed that Connaraceae are sister to Oxalidaceae (Nandi *et al.* 1998). These two families share the presence of heterostyly, benzoquinone rapanone, and extegmic seeds (Nandi *et al.* 1998), though Connaraceae are mainly a woody family and Oxalidaceae mainly herbaceous. The family is further subdivided into two subfamilies on the bases of the presence or absence of endosperm. Subfamily Jolydoroideae Gilg are further subdivided into three tribes of which both genera in the FSA-region belong to tribe Cnestideae Planch. (Lemmens *et al.* 2004; Reveal 2012).

Heterostyly is reported from  $\pm$  25 angiosperm families and is a floral device that promotes outcrossing, hence reducing the harmful effects of close inbreeding within a plant population (Barrett 1992). Tristyly has been claimed repeatedly as typical of the Connaraceae, with distyly and dioecy as derived conditions produced by sterilization of androecial or carpellary parts (Baker 1962). Tristyly is known to occur only in Amaryllidaceae, Lythraceae, Oxalidaceae, Pontederiaceae, Connaraceae (Barrett 1993) and Linaceae (Thompson *et al.* 1996).

The cuticle waxes of Connaraceae are morphologically similar to those of Fabaceae (Fabales) (Ditsch *et al.* 1995), with which Connaraceae have frequently been confused. However, the two are not particularly close,

and can usually be distinguished because the Connaraceae lack stipules and have rather small, polysymmetric flowers with ten stamens of two different lengths, a combination of features unknown in Fabaceae (Leenhouts 1958a).

The plants are often poisonous (Mabberley 2008). The irritating hairs on the pods of *C. polyphylla* produce severe itching when touched (Watt & Breyer-Brand-wijk 1962). The family is of little economic importance. *Cnestis ferruginea* Vahl ex DC. is a shrub widely used in traditional African medicine for the treatment of various painful and inflammatory conditions (Ishola *et al.* 2011).

The flowers are reported to be faintly scented, with a wide diversity in forms of heterostyly accompanied by a self-incompatibility system, and are most likely pollinated by insects such as bees (Leenhouts 1958a). Connaraceae have strikingly coloured, dehiscent fruits with bicoloured seeds that are dispersed by birds or by small animals on the forest floors (Lemmens *et al.* 2004).

## MATERIAL AND METHODS

Two taxa were studied from herbarium specimens housed in PRE. The most important type specimens were accessed on websites, which are cited below. Acronyms for herbaria are listed in Holmgren *et al.* (1990).

## TAXONOMY

**Connaraceae R.Br.** in J.H. Tuckey, Narrative of an expedition to explore the river Zaire: 431 (1818); Gilg: 61 (1894); Schellenb.: 31 (1915); Mendes: 615 (1966); Breteler: 1 (1989); Jordaan: 229 (2000); Lemmens *et al.*: 74 (2004).

Evergreen or deciduous woody climbers, climbing by means of the winding ends of young branches, less often shrubs, small trees or a rhizomatous shrublet. *Stipules* absent. *Leaves* alternate, compound, unifoliate, ternate, or imparipinnate in FSA-region; leaflets sub-opposite or alternate, entire; petiole pulvinate at base, transversely ridged. *Inflorescences* axillary or terminal racemes, panicles, or rarely fascicles. *Flowers* bisexual, or rarely unisexual, regular, 5-merous. *Sepals* imbricate or valvate, free or connate at base, caducous or often persistent and sometimes accrescent in fruit to strongly so. *Petals* free or slightly connate to middle, imbricate or rarely valvate. *Stamens* 10, in 2 whorls, free or connate at base, the 5 outer epispalous ones longer than 5 inner epipetalous ones; filaments free or united basally into short tube; anthers dorsifixed, 2-thecous, dehiscent

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longitudinally, introrse. *Gynoeceum* superior, of 5, free, hairy, 1-locular carpels; ovules 2, collateral, nearly basal to nearly apical. *Fruit* of 5 follicles, sometimes connate at base, dehiscing by ventral suture. *Seeds* 1(2) per follicle, with or without endosperm; hilum lateral to basal; testa partly to entirely fleshy; sarcotesta (aril or pseudo-aril) sometimes partly free.

Genera 12,  $\pm$  110–200 spp. (Lemmens *et al.* 2004), pantropical in Central and South America, Africa, Madagascar, Southeast Asia, Malesia, Australia and the Pacific islands (Heywood *et al.* 2007); five genera and 110 spp. in the Neotropics (Forero 2012); nine genera and 48 spp. in sub-Saharan Africa (Klopper *et al.* 2006); five genera and 11 spp. in Madagascar (Madagascar Catalogue 2012); six genera and nine spp. (one endemic) in China (Lingdi & Turland 2003); six genera and  $\pm$  40 spp. in Malesia (Leenhouts 1958a); two genera and two spp. in Australia (Australian Tropical Rainforest Plants); two genera and two spp. occur naturally in southern Africa.

#### Key to genera for FSA-region (after Jordaan 2000)

Leaflet apex tapering, base asymmetric; flowers in terminal or axillary racemes, often clustered in old leaf bases (cauliflorous); follicles velvety,  $\pm$  rostrate; seed with endosperm, seed coat 2-coloured ..... *Cnestis*

Leaflet apex rounded, base symmetric; flowers in few-flowered, axillary racemes, usually produced before leaves; follicles glabrous or glabrescent, mostly acute to rounded apically; seed without endosperm, seed coat entirely fleshy and red ..... *Rourea*

***Cnestis* Juss.** in A.L. de Jussieu, *Genera plantarum secundum ordines naturales disposita*: 374 (1789); DC.: 86 (1825); Endl.: 1140 (1840); Sonder: 527 (1860); Hook.: 433 (1862); Gilg: 67 (1894); Burtt Davy: 511 (1932); Hemsl.: 2 (1956); Mendes: 615 (1966); Lemmens: 174 (1989). Type species: *C. polyphylla* Lam., fide Lemmens (1989).

Woody climbers, shrubs or rarely small trees; branches cylindrical, hairs multicellular. *Leaves* imparipinnately compound, alternate; leaflets opposite or alternate, often asymmetric and often also acuminate. *Inflorescences* racemose, or occasionally in panicles, fascicles, or flowers solitary on main stem, axillary, usually more than 1 together in axil of single leaf, sometimes pseudoterminal. *Flowers* bisexual or unisexual with some bisexual, small, hairy, heterostylous, often heterodistylous, white, yellowish or tinged red; pedicels with distinct joint. *Sepals*  $\pm$  free, imbricate in bud. *Petals* shorter, as long as, or somewhat longer than sepals, free, imbricate in bud, hairless or with some hairs outside near base. *Stamens* with filaments free or shortly connate at base, glabrous, outer slightly longer than inner; anthers usually recurved with age. *Gynoeceum* of 5, free, sessile carpels; ovules (1)2 per locule; styles often pilose at base, short, included; stigmas capitate. *Fruit* 1–5 follicles per flowers, reniform or cylindrical, curved or undulated, beaked or not, opening lengthwise along ventral suture, densely hairy and sometimes also with long rigid hairs outside and with rigid, easily detached, stinging hairs inside. *Seed* 1, attached to base of follicle, ovoid, with yellow to red sarcotesta at base,

surrounding hilum; testa black and glossy; endosperm present, abundant.

Genus of  $\pm$  13 spp., largely restricted to tropical Africa and Madagascar, but one or two in tropical Asia; 1 sp. in southern Africa, usually found in rain forest and savanna.

*Etymology*: *Cnestis* is derived from the Greek word *knesiao* = to itch, and *knestis* = a rasp, referring to the hairs on the fruits which cause itching when touched (Glen 2004).

***Cnestis polyphylla* Lam.**, *Encyclopedie Methodique*, *Botanique* 3: 23, pl. 387 (1789); Planch.: 440 (1850); Schellenb.: 13 (1910); Lemmens: 220 (1989); Beentje: 434 (1994); M.Coates Palgrave: 252 (2002); Lötter: 142 (2002); Boon: 132 (2010). Type: Madagascar, *Commerson s.n.* [P-JU—digital image, lecto.!, designated by Lemmens: 220, 224 (1989); MPU—digital image!, isolecto.].

*C. glabra* Lam.: 23 (1789); DC.: 87 (1825); Planch.: 440 (1850); Schellenb.: 13 (1910); Schellenb.: 318 (1938). Type: Mauritius, *Commerson* 599 [P P00364940—digital image, lecto.!, designated by Schellenberg: 40 (1938); L, isolecto.].

*Zanthoxylum natalense* Hochst.: 304 (1844). *Cnestis natalensis* (Hochst.) Planch. & Sond.: 528 (1860); Gilg: 215 (1896); Schellenb.: 14 (1910); Baker f.: 50 (1911); Schellenb.: 318 (1915); Burtt Davy: 511 (1932); Schellenb.: 40 (1938); Mendes: 616 (1966); Mendes: 2 (1969). Type: South Africa, KwaZulu-Natal, between Umlaas River and Durban [Port Natal], 1840, *Krauss* 60 [K—digital image, holo.!, fide Lemmens (1989)].

*Omphalobium?* *discolor* Sond.: 24 (1850). Type: South Africa, KwaZulu-Natal, Durban [Port Natal], *Gweinzius* 54 & 577 (?S, syn.).

*Cnestis polyphylla* var. *bullata* Baill.: 243 (1867). *Cnestis bullata* (Baill.) Baill.: t. 17 (1886). Type: Madagascar, St Marie Island, *Boivin* 1889 (P, holo.).

*C. lurida* Baill.: 244 (1867); Schellenb.: 15 (1910). Type: Madagascar, Nossi-Bé Island, December 1851, *Boivin s.n.* (P P00364937—digital image, holo.!).

*C. boiviniana* Baill. ex Schellenb.: 39 (1938); Keraudren: 18 (1958). Type: Madagascar, St Marie Island, *Boivin s.n.* (P—digital image, holo.!).

*Nomenclatural note*: Lemmens (1989) gives no reason for changing the author citation of *C. natalensis* (Hochst.) Planch. ex Sond., formerly Planch. & Sond. (Mendes 1966). Hochstetter (1844) originally described this plant in the genus *Zanthoxylum*, which belongs to the Rutaceae, and it was not mentioned by Planchon (1850) in his monograph of Connaraceae. The combination was published ten years later in Sonder's (1860) account of Connaraceae in Harvey & Sonder's *Flora capensis*, where he stated the author citation clearly as Planch. & Sond.; a citation which I follow here. Sonder presumably saw Planchon's (1850) monograph on the



Connaraceae, which was published in the same volume of *Linnaea* in which Sonder (1850) himself published *Omphalobium discolor* for the same entity, but only later connected Hochstetter's plant with the Connaraceae.

Shrub, robust climber or small tree with trailing branches, up to 4 m tall, multi-stemmed, much-branched; branches cylindrical, 10–25 mm in diam., usually distinctly lenticellate, densely brown hairy at first becoming almost hairless with age. *Leaves* crowded towards ends of branches, imparipinnately compound, alternate, 3–9(–14)-jugate; leaflets opposite, subopposite or alternate, slightly overlapping, thinly leathery, dark green above, much paler below, glabrous above, glabrescent below with scattered hairs confined to midrib and veins; leaflet lamina obovate to oblong, 20–40 × 9–15 mm, apex obtuse to acute or abruptly acuminate, base asymmetric, obliquely rounded to truncate or shallowly cuneate, margin entire, midrib and lateral veins sunk above, prominently raised beneath, lateral veins looping near margin, reticulate tertiary venation conspicuous on both sides; rachis 60–180(–250) mm long, with cinnamon hairs; petiole up to 100 mm long; petiolule up to 2 mm long, hairy. *Inflorescences* racemose, 5–30-flowered, 40–80(100) mm long, axillary or pseudoterminal, much shorter than leaves, densely hairy; bracteate, bracts densely hairy. *Flowers* small, heterostylous, whitish green or greenish yellow, on old wood, usually borne below leaves, bisexual or unisexual. *Sepals* narrowly triangular, ± 2–5 × 1–2 mm, free, reflexed, brown pilose outside. *Petals* narrowly elliptic to narrowly obovate, (1.5–)3.5–4.5 × 0.5–1.5 mm, free, spreading, truncate or retuse, glabrous or with some long hairs in basal part outside. *Stamens* 10, in 2 whorls, free or connate at base, slightly differing in length, 1–4 mm long; anthers ± 0.5 × 0.4 mm, *Gynoecium* of 5, free, sessile carpels; ovary 0.5–1.0 mm long, yellowish, pilose; ovules (1)2 per locule; style straight or recurved, pilose in basal part, included; stigma usually oblique, 2-lobed. *Follicles* 1(–5), obliquely pear-shaped, 15–25 × 7–10 mm, with a curved or twisted beak up to 4 mm long, covered with irritating yellowish hairs inside, sparsely hairy outside, apricot-coloured when ripe, ventrally dehiscent. *Seed* 1, ovoid, 8–18 × 3–9 mm, glossy black; sarcotesta yellow, 3–9 mm long, ruminate (Figure 1).

**Taxonomic note:** Lemmens (1989) has a very broad species concept of this taxon, occurring in three well disjunct areas: (i) Madagascar, Mauritius and Reunion; (ii) Kenya; and (iii) southern Africa (including Zimbabwe and Mozambique). The southern African component of this taxon was formerly known as *Cnestis natalensis* (Hochst.) Planch. & Sond, e.g. Burt Davy (1932), Mendes (1966, 1969), Ross (1972), and differs from Malagasy material in its glabrescent, smaller leaflets, 20–40 mm long (vs. mostly longer than 50 mm, occasionally 40 mm long) very oblique and truncate bases. Madagascar specimens have leaflets with mostly symmetric, cordate to subcordate bases, and the indumentum varies from pilose to pubescent on the undersurface of the leaflets, although the inclusion of *C. glabra* indicates some glabrous forms. Specimens from mainland southern African also have relatively broader sepals, up to 5 mm wide at base, and often pilose inside, and the follicles are distinctly beaked. Madagascar

specimens have narrower sepals, 1–2 mm wide, glabrous inside, and the follicles are truncate and usually not distinctly beaked. Lemmens (1989: 224) argued that material from an isolated population in Kenya bridges the differences in characters of leaflets, sepals and fruits between Africa and Madagascar, which makes it impossible to maintain the South African taxon as distinct. Unfortunately, no material of the Kenyan population at Mombasa are housed in the National Herbarium in Pretoria (PRE) and morphological differences could not be studied. This needs further investigation. If three distinct species are involved, the Kenya plants require a new name, and southern African material will revert to *C. natalensis*. Alternatively, differences could be recognized at least at subspecific rank.

**Common names:** itch-pod, *jeukpeul* (Afrikaans), *monèpènèpè* (Northern Sotho), *lihlozi* (Swazi), *ihlozi* (Zulu) (Van Wyk *et al.* 2011).

**Distribution and habitat:** eastern parts of southern Africa from Limpopo to the Eastern Cape as far south as Kentani and northwards to Eastern Zimbabwe and adjacent Mozambique on the Chimanimani Mountains (Figure 2), with a population in Mombasa on the Kenyan coast; also in Madagascar, Mauritius and Reunion. It grows as understorey component in coastal, lowland or escarpment forest, on rocky slopes at low to medium elevations.

#### *Selected specimens*

ZIMBABWE.—2032: Mannicaland, Chipinge Dist., Farm Brabant, Rusitu Valley, (–AA), *Van Wyk BSA1045, BSA1232*.

LIMPOPO.—2229 (Waterpoort): Louis Trichardt, Hanglip Forest Reserve, (–DD), *Van Wyk 5987*. 2230 (Messina): Venda, Khalavha, (–CD), *Mbedzi 1564*; Zoutpansberg Dist., Makonde Mission Station, 15 miles NE of Sibasa, (–DC), *Codd 6861*. 2330 (Tzaneen): Zoutpansberg Dist., on Tzhakoma, Entabeni Forest Reserve, (–AB), *Poynton PRE54918*.

MPUMALANGA.—2430 (Pilgrim's Rest): Mariepskop, (–DB), *Van der Schijff 4733, 5058, 6217*. 2530 (Lydenburg): Lydenburg Dist., Witklip, (–BD), *Kluge 581*.

SWAZILAND.—2531 (Komatipoort): Piggs Peak, (–CD), *Compton 31560*.

KWAZULU-NATAL.—2732 (Ubombo): Ingwavuna Dist., Gwalweni Forest [Hlatikulu Forest], (–AC), *Stephen 776*; Sodwana Bay, Sibayi area, (–BC), *Van der Schijff 6586A*. 2831 (Nkandla): Eshowe, (–CD), *Thode A1230*; Ngoye Forest Reserve, (–DC), *Venter 2253*. 2832 (Mtubatuba): Hlabisa Dist., Hluhluwe Game Reserve, (–AA), *Ward 2830*. 2930 (Pietermaritzburg): 9 miles NW of New Hanover, (–BC), *Codd 1441*; Pietermaritzburg, Table Mountain, (–CB), *Killick 85*. 2931 (Stanger): 2 miles W of Stanger, (–AD), *Moll 2198*. 3030 (Port Shepstone): Umzinto Dist., Vernon Crookes Nature Reserve, (–BC), *Balkwill & Cadman 2212*. 3130 (Port Edward): Umtamvuna Reserve, Braemar Farm, (–AA), *Nicholson 1599*.

EASTERN CAPE.—3029 (Kokstad): Mount Auliff, Fort Donald, (–CD), *Sim 2369*; Bizana Dist., (–DD), *Acocoks 10937*. 3129 (Port St Johns): Egossa, (–BC), *Srey 8924*; Mkambati Reserve, Daza Forest, (–BD), *Brand et al. 353*; Umgazi River Mouth, (–CB), *Pienaar 133*; Port St Johns Dist., Umzimvubu River Valley, (–DA), *Balkwill et al. 1883*. 3228 (Butterworth): Kentani, (–CB), *Pegler 803*.

**Rourea Aubl.** in *Histoire des plantes de la Guiane Française*: 467 (1775), name conserved against *Kala-wael* Adanson (Leenhouts 1958b); Juss.: 369 (1789); Baill.: 228 (1867); Jongkind: 310 (1989). Type species: *R. frutescens* Aubl.



FIGURE 1.—*Cnestus polyphylla*. A, flowering branch,  $\times 1$ ; B, leaflet with asymmetric base,  $\times 1$ ; C, short-staminate flower,  $\times 4$ ; D, flower in cross section,  $\times 8$ , A–D from Pegler 803; E, mature beaked follicle with extruding seed,  $\times 2$ ; F, seed with pseudo-aril (sarcotesta),  $\times 2$ , E & F from Mthonti 1b. Artist: Marguerite Scott.



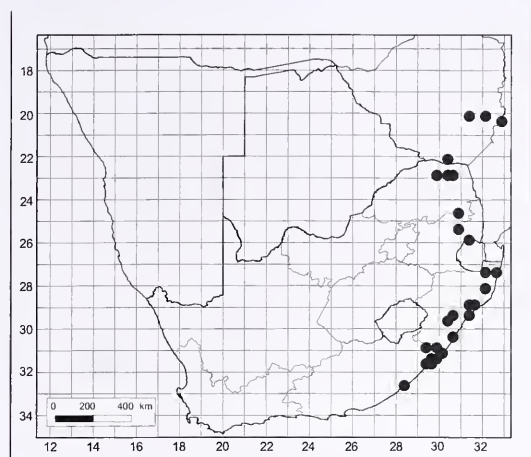


FIGURE 2.—Distribution of *Cnestis polyphylla* in southern Africa.

*Byrsocarpus* Schumach.: 226 (1827). Type species: *B. coccineus* Schumach. & Thonn. (1827), lecto., designated by Schellenb.: 146 (1938).

Climbers, shrubs or trees; branches cylindrical or clearly lobed, often ending in a tendrilloid tip, usually with lenticels. *Leaves* imparipinnately compound, leaflets opposite or subopposite, usually  $\pm$  symmetric. *Inflorescences* axillary, paniculate or racemose, sometimes 1–more together at end of leafy branch, forming a terminal synflorescence. *Flowers* bisexual, heterodistylous, white, tinged yellow or red, sweet-scented, produced before leaves; pedicel always with a distinct joint. *Sepals* free or almost completely connate, imbricate in bud, ciliate, persistent and accrescent soon after pollination. *Petals* as long as to much longer than sepals, free or connate at base, often inrolled or folded, hairless or with few apical hairs. *Stamens*: filaments connate into a short tube, hairless. *Gynoecium* of 5, free carpels; ovules 2, basal; style terete; stigmas  $\pm$  capitate. *Fruit* a follicle, 1–5 per flower, ovate to elliptic with rounded to acute apex or beaked, hairless or velutinous, with orange to red glandular hairs outside, hairless inside, with persistent calyx, dehiscing by a ventral suture or circumscissile at base. *Seed* solitary, rarely 2 per follicle, subovoid to ellipsoid, completely or partially enclosed in a brightly coloured sarcotesta (aril) fused with the partly to almost totally fleshy testa; hilum basal, without endosperm.

Genus of  $\pm$  68 spp., in tropics in Old and New World, in forests and savanna; 48 spp. in Neotropics, Mexico to Brazil (Forero 2004, 2012: Neotropical Connaraceae website); eight spp. in Sri Lanka and Malesia, Australia and Melanesia (Leenhouts 1958a); 12 spp. in tropical Africa and Madagascar (Klopper *et al.* 2006); one species in southern Africa.

*Note*: the southern African species was formerly treated in regional Floras in the genus *Byrsocarpus* (e.g. Hemsley 1956; Mendes 1966, 1969). Since Jongkind (1989) revised the genus for the whole of Africa, he placed *B. orientalis*, originally described by Baillon (1867) based on a plant collected in Kenya, into *Rourea orientalis*. He further divided *Rourea* into five sections,

placing the southern African species in sect. *Byrsocarpus* (Thonn. ex Schumach.) Jongkind.

*Etymology*: *Rourea* is derived from Aroura parish, French Guiana (Glen 2004). The type species, *R. frutescens*, was first described from French Guiana by Aublet (1775), who was a French explorer and botanist and founder of the knowledge of the flora of Guyana (Stafleu & Cowan 1976–1988).

***Rourea orientalis* Baill.** in *Adansonia* 7: 230 (1867); Keraudren: 4 (1958); Jongkind: 310 (1989); M.Coates Palgrave: 252 (2002); Curtis & Mannheimer: 118 (2005). *Byrsocarpus orientalis* (Baill.) Baker: 452 (1868); Schellenb.: 42 (1910); Hemsl.: 17 (1956); Mendes: 624 (1966); Mendes: 6 (1969). Type: Kenya, Mombasa, *Boivin s.n.* (P—digital image, holo!).

*Byrsocarpus tomentosus* Schellenb.: 452 (1919); Troupin: 92 (1952). Type: Tanzania, Songea, *Busse 804* (B—digital image, holo!; EA—digital image!, G—digital image!, iso.).

*Byrsocarpus usambaricus* Schellenb.: 154 (1938). Type: Tanzania, E Usambara, Longusa-Sigital, *Peter 40014* (B—digital image, holo!).

Scrambling shrub, climber, or tree up to 6 m tall; young branchlets densely to sparsely hairy, reddish brown or grey-brown, with conspicuous raised lenticels. *Bark* smooth, mottled brown-purple. *Leaves* drooping on rachis, compound, 6–14-jugate, up to 200 mm long, glabrous above, hairless or with scattered hairs below, bright green above, paler beneath; leaflet lamina elliptic to elliptic-oblong, 12–40  $\times$  7–19 mm, apex obtuse-aristate, base rounded to broadly cuneate, margin entire, midrib sometimes densely hairy; rachis up to 250 mm long. *Inflorescence*: rachis up to 50 mm long, hairless or hairy. *Flowers* white to pale yellow, up to 30 mm in diam., sweetly lemon-scented. *Sepals* ovate, up to 3  $\times$  2 mm, puberulous, hairs especially dense on midvein and margins. *Petals* narrowly elliptic, 7–11  $\times$  1.5–3.5 mm, membranous, sometimes folded at top, glabrous. *Stamens* 10; long-staminate flowers with longer stamens  $\pm$  7 mm long and shorter stamens  $\pm$  4 mm long; short-staminate flowers with longer stamens  $\pm$  3 mm long and shorter stamens  $\pm$  2 mm long; filament-tube 1–2 mm long. *Ovary* ovoid,  $\pm$  1 mm long, densely hairy; styles of long-staminate flowers up to 1.5 mm long, usually recurved; styles of short-staminate flowers to 4.5 mm long. *Follicle* 15–23  $\times$  5–12 mm, symmetrical, apically rounded, red-brown, glabrous, calyx spreading at maturity. *Seed* up to 15  $\times$  8 mm, completely enclosed in a bright red pseudo-aril (Figure 3).

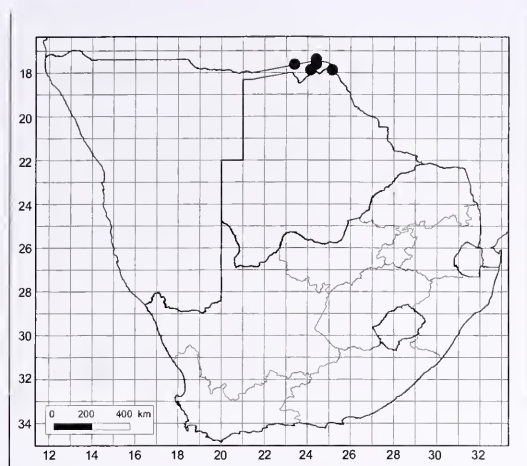
*Common names*: shortpod, kortpeul (Afrikaans), mukolwe (Lozi) (eastern Caprivi Strip), chidzimamuriro (Manyika, Ndau) (Manicaland in Zimbabwe and Mozambique), nhantsanga (Sena) (Mozambique, Sofala and Tete Provinces) (Van Wyk *et al.* 2011).

*Distribution and habitat*: in the FSA-region only in the extreme northeastern corner of Botswana and the Caprivi Strip of Namibia, extends northwards to Eastern Angola and southeast Democratic Republic of Congo (DRC), and eastwards through Zambia, Malawi, Zimbabwe and Mozambique to Tanzania (including Zanzi-





FIGURE 3.—*Rourea orientalis*. A, leafless flowering branch,  $\times 1$ , from Miller B/1099; B, fruiting branch,  $\times 1$ ; C, portion of bark showing lenticels,  $\times 3$ , B & C from Killick 3389; D, long-staminate flower with stamens of two lengths and pistils in cross section,  $\times 6$ ; E, sepal,  $\times 6$ ; F, petal,  $\times 6$ ; G, gynoecium,  $\times 6$ ; H, carpel cut open showing ovules and recurved style in cross section,  $\times 2$ , D–H from Miller B/1099; I, mature follicle with extruded seed,  $\times 2$ ; J, seed completely covered by pseudo-aril,  $\times 2$ , I & J from Killick 3389. Artist: Marguerite Scott.

FIGURE 4.—Distribution of *Rourea orientalis* in FSA-region.

bar) and Kenya; also in Madagascar (Keraudren 1958). It grows on margins of thicket, savanna or woodland in riverine vegetation, floodplains, often on termitaria, on sandy loam or alluvial soil. For tropical African distribution see Figure 171 in Jongkind (1989) for FSA distribution see Figure 4.

#### Selected specimens

NAMIBIA.—1723 (Singalawwe): Western Caprivi Strip, Kwando Flood Plain, (–CB), *Tinley 1530*. 1724 (Katima Mulilo): Katima Mulilo, S of Hippo Lodge, (–AD), *Venter et al. 92*; on small track between Katima Mulilo and Kwena village, (–CB), *Hines 1120*; Maningi Manzi, (–CC), *Miller 1704*. 1725 (Livingstone): Impalela Island, (–CC), *Pienaar & Vahrmeyer 198*.

BOTSWANA.—1725 (Livingstone): Chobe Dist., between Kasane and Kazungula, (–CC), *Miller B/1129*.

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# A taxonomic revision of the small Cape genus *Steirodiscus* (Asteraceae: Senecioneae)

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**Keywords:** Asteraceae, Senecioneae, *Steirodiscus* Less., southern Africa, taxonomy

## ABSTRACT

The genus *Steirodiscus* Less. is revised, with full descriptions, nomenclature, illustrations and distribution data. Five species are recognised in two sections: sect. *Steirodiscus* with free involucre bracts and sect. *Psilothomma* with bracts connate into a smooth cup. *S. linearilobus* DC. is established as an earlier name for *S. schlechteri* Bolus, which is relegated to synonymy.

## INTRODUCTION

*Steirodiscus* Less. is a minor genus of Senecioneae comprising five species of small, wiry annuals, all endemic to the Greater Cape Floristic Region (Goldblatt & Manning 2000; Herman *et al.* 2000). Currently included in subtribe Senecioninae (Pelser *et al.* 2010), its relationships within the subtribe are still unclear (Nordenstam *et al.* 2009). Although treated as one of the ‘othonnoid’ genera by Jeffrey (1992) on account of its ebracteolate and sometimes gamophyllous involucre, molecular data place it among the group of genera that includes *Bolandia* Cron, *Cineraria* L., *Emilia* Cass., *Mesogramma* DC. and *Stilpnogyne* DC., rather than with the Othonninae (Nordenstam *et al.* 2009; Pelsner *et al.* 2010). A recent phylogenetic analysis of plastid and nuclear sequence data identifies *Steirodiscus* as one of several lineages with strongly incongruent positions in the two analyses (Pelser *et al.* 2010). Hybridization and incomplete lineage sorting were suggested as explanations for the incongruence.

*Steirodiscus* was established by Lessing (1832) to accommodate the species described by Linnaeus fil. (1782) as *Cineraria capillacea*, and was originally characterised by a uniseriate involucre of free bracts without associated bracteoles, female ray florets with pubescent cypselas, and male-fertile disc florets. At the same time Lessing (1832) also recognised the genus *Gamolepis* for four shrubby Cape species now treated in *Euryops* plus the solitary annual species *Othomma tagetes* L. (under the illegitimate superfluous name *Gamolepis amua* Less.), which were linked by their smooth, cup-shaped involucre, female ray and bisexual disc florets, and epappose cypselas.

These generic circumscriptions were followed by Candolle (1838), who added a second species, *Steirodiscus linearilobus* DC. The sole annual species of *Gamolepis*, *G. tagetes* (L.) DC., which had by then been selected as the lectotype of the genus (Pfeiffer 1874), was subsequently transferred to *Steirodiscus* by Schlechter (1899), who was struck by its marked similarity to that genus in habit, finely dissected leaves and epappose cypselas, despite the marked difference in their involucre. At this time two further species were described, *S. gamolepis* Bolus and *S. schlechteri* Bolus (Schlechter 1899), bringing the total in the genus to five. A sixth species [now *S. speciosus* (Pillans) B.Nord.] was later named by Pillans (1931) under the generic name *Gamolepis*.

*Steirodiscus* is defined by its annual habit, pinnatisect or bipinnatisect leaves with subsecund, linear-filiform segments, and solitary or laxly corymbose, radiate capitula with uniseriate, ebracteolate involucre, and all florets lacking a pappus. The involucre bracts may be free or connate into a smooth cup. The generic name is derived from the sterility of the disc florets in *S. capillaceus* (Lessing 1832), but this condition is not easily assessed in flowering capitula as maturation of the central florets is tardy. We have confirmed that the central disc florets in *S. tagetes* fail to develop fruit but whether this is due to congenital sterility or to nutritional constraints we cannot say. This will need to be assessed through careful anatomical investigation for the presence or absence of an embryo in the central disc florets.

A brief review of the group under the illegitimate superfluous generic name *Psilothomma* (E.Mey. ex DC.) E.P.Phillips (Nordenstam 1968) was presented by Phillips (1950), who also provided a key to the five species recognised. This review, although based on very few collections, provided some much-needed clarity in the genus but Phillips (1950) inexplicably overlooked Candolle’s (1838) *S. linearilobus*. This name was applied (incorrectly as we show below) by Hutchinson (1946) to plants from the Klein Roggeveld and the species has remained poorly understood until now.

Five names in *Steirodiscus* are included in the Red List of South African Plants (Raimondo 2009), four as either EN or VU and *S. linearilobus* as DD signifying its uncertain identity. At the moment therefore, although

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six names are validly published in the genus, only five species are accepted (Goldblatt & Manning 2000). The genus is urgently in need of revision, not only to establish the number of recognised species and the application of the available names, but also the distribution and thus conservation status of the taxa. Three of the species (*S. gamolepis*, *S. linearilobus* and *S. speciosus*) are highly localised endemics and another (*S. tagetes*) is restricted to the West Coast, where it is evidently already extinct from part of its range and threatened by coastal development elsewhere. The fifth species (*S. capillaceus*), although relatively widespread, has not been recorded from most of its historical range for over 50 years.

We provide a complete taxonomic revision of *Steirodiscus*, including full descriptions and synonymy, illustrations and distribution data for all species. The species fall into two groups depending on whether the involucre bracts are free to the base or connate into a smooth cup, which we treat as the sections *Steirodiscus* and *Psilothonna* respectively.

#### MATERIALS AND METHODS

Specimens or digital images of all relevant types were examined, as well as all herbarium material from BOL, NBG, PRE and SAM (acronyms after Holmgren *et al.* 1990), the primary collections of species from southern Africa. All species were also located and studied in the field.

#### TAXONOMY

***Steirodiscus* Less.**, Synopsis generum Compositarum: 251 (1832). Type species: *S. capillaceus* Less.

*Gamolepis* Less.: 251 (1832). Type species: *G. tagetes* (L.) DC. (= *S. tagetes* (L.) Schltr.), lecto. designated by Pfeiffer: 1406 (1874).

*Psilothonna* (E.Mey. ex DC) E.P.Phillips: (1950), nom. illegit. superfl. pro *Gamolepis* Less. *Gamolepis* sect. *Psilothonna* E.Mey ex DC.: 40 (1838). Type species: *P. tagetes* (L.) E.P.Phillips = *S. tagetes* (L.) Schltr.

Small, subglabrous annual herbs with flexuose, wiry stems. *Leaves* alternate, sessile, pinnatisect or bipinnatisect with subsecund linear to filiform lobes, or uppermost leaf simple and filiform, mucronulate, arachnoid in axils and on inner face of petiole when young. *Capitula* pedunculate, solitary on ultimate branches, usually forming lax corymbs; peduncles slender and wiry but widening and fistulose apically, with 1–3 scattered, minute, scale-like bracts. *Involucre* ecalyculate, subglobose to campanulate-obconic, bracts either free or connate  $\pm$  two-thirds into smooth cup. *Receptacle* convex, epaleate. *Ray florets* female, bright yellow to orange-yellow, corolla tube cylindrical, sparsely pubescent on outer surface with multicellular trichomes often concentrated near top of tube, limb oblong, 2–4 times as long as tube, 4(5)-veined, apically 3(4)-toothed. *Stigmas* linear-oblong, with sterile apical appendage. *Disc florets* bisexual, evidently fertile but central florets sometimes

not developing mature fruits, yellow, corolla narrowly funnel-shaped, 5-lobed, sparsely pubescent or rarely glabrous, lobes suberect, ovate. *Anthers* ecalcarate and ecaudate, with lanceolate apical appendage. *Style* terete, branches linear-oblong, margins stigmatic, apices conical with ring of sweeping hairs. *Cypselas* obovoid or oblong, obscurely 5-angled and 10-ribbed, glabrous or pubescent. *Pappus* 0.

5 spp., South African west coast and near interior.

#### Key to species

- 1a Involucral bracts free to base, canaliculate (sect. *Steirodiscus*) ..... 2
- 2a Uppermost leaves filiform; involucre bracts and ray florets 8–12; ovaries and cypselas sparsely or densely puberulous; disc florets puberulous on lobes ..... *S. capillaceus*
- 2b Uppermost leaves pinnatisect or filiform; involucre bracts and ray florets 13–16; ovaries and cypselas glabrous; disc florets glabrous ..... *S. linearilobus*
- 1a Involucral bracts connate for most of length into smooth cup (sect. *Psilothonna*) ..... 3
- 3a Leaves mostly 10–20 mm long with up to 3 pinnae; involucre 3.5–4.5 mm long; ray florets 4–8, half as many as involucre lobes; ovaries and cypselas pubescent ..... *S. gamolepis*
- 3b Leaves mostly 20–60 mm long with up to 8 pinnae; involucre 5–8 mm long; ray florets 8–15,  $\pm$  as many as involucre lobes; ovaries and cypselas glabrous ..... 4
- 4a Involucre mostly 4–5 mm diam., campanulate; ray floret trichomes compound or lobed,  $\pm$  coalescent into fleshy, fimbriate collar at top of tube ..... *S. tagetes*
- 4b Involucre mostly 2–3 mm diam., urceolate and constricted above ovaries when dry; ray floret trichomes simple,  $\pm$  scattered at top of tube ..... *S. speciosus*

#### Sect. *Steirodiscus*

Stems strongly flexuose (zig-zag); involucre cylindrical or subglobose with bracts free to base and canaliculate.

1. ***Steirodiscus capillaceus* (L.f.) Less.**, Synopsis generum Compositarum: 251 (1832). *Cineraria capillacea* L.f.: 375 (1782). *Psilothonna capillacea* (L.f.) E.P.Phillips [as *P. capillacea* (Less.) E.P.Phillips]: 17 (1950). Type: South Africa, ‘Cap. B. Spei’ [‘in arenosis Swartland’ *fide* Thunberg 1823], *Thunberg s.n. UPS-THUNB 19907* (UPS-THUNB, holo.—microfiche!).

*Steirodiscus linearilobus* sensu Hutch.: 140 (1946), non DC.

Annual herb, 60–200 mm, stem strongly flexuose, corymbosely branched above or rarely below. *Leaves* alternate, ascending, mostly 15–40(–60)  $\times$  8–20 mm, pinnatisect or some leaves bipinnatisect, with up to 8 lobes on each side, lobes alternate or subopposite and subsecund, filiform to linear, 3–10  $\times$  0.5 mm, entire or with 1 or 2 lobules, rarely median lobe markedly prolonged, uppermost leaf simple and filiform. *Capitula* solitary, pedunculate; peduncles 15–60 mm long, with 2 or 3 minute, scale-like bracts. *Involucre* subglobose, 4–5  $\times$  4–5(–10) mm, bracts 8–12, free, convex abaxially and canaliculate adaxially, leathery and three-veined in basal two-thirds, with membranous margins, penicillate. *Ray florets* as many as involucre bracts and opposite them, yellow; tube cylindrical, 1.5 mm long, with scattered abaxial trichomes; blade (5–)7–10(–15)  $\times$  1.5–3.0 mm, spreading, recurved apically; ovary ellipsoid, 1.5

mm long, antrorsely densely puberulous, style branches partly exerted, 0.5 mm long. *Disc florets* fertile, yellow, 4.5 mm long; tube funnel-shaped,  $\pm 2$  mm long; lobes  $\pm 1$  mm long, ovate, sparsely puberulous, acute; ovary ellipsoid, 1.5 mm long, antrorsely densely puberulous, style branches 0.5 mm long. *Cypselas* obovoid,  $\pm 1.5$  mm long, densely antrorsely pubescent. *Flowering time*: Aug.–Sept. Figure 1.

*Distribution and ecology*: *Steirodiscus capillaceus* is the most widely distributed species in the genus, with a curiously scattered range along the West Coast from Hopefield to the foot of Pikenierskloof Pass, in the northern Cedarberg and Bokkeveld Mountains, and further inland on the Klein Roggeveld at the foot of the Komsberg Pass (Figure 2). It favours sandy loam soils, typically in renosterveld shrubland.

*Diagnosis and relationships*: *Steirodiscus capillaceus* shares free involucre bracts with *S. linearilobus*, but is distinguished by the puberulous ovaries and cypselas, and by the sparsely puberulous corolla lobes of the disc florets. The uppermost leaves are invariably filiform.

*Conservation status*: although relatively widespread historically, *Steirodiscus capillaceus* has not been recorded from the Hopefield–Piketberg–Eendekuil and Bokkeveld localities for over sixty years and appears to be extinct there, likely as a result of agricultural expansion. The only recent records are from the Klein Roggeveld at the foot of the Komsberg Pass, where it is still relatively plentiful.

#### Additional specimens seen

NORTHERN CAPE:—**3119** (Calvinia): top of Vanrhyn's Pass, (–AC), 3 Sept. 1948, *R.H. Compton* 20878 (NBG); sandy flats, (–AC), 12 Aug. 1961, *G.J. Lewis* 5898 (NBG). **3220** (Sutherland): Klein Roggeveld, near Farm De Kom, (–DA), 15 Sept., 2004, *D.A. Snijman* 1951 (NBG); 9.5 km S of top of Komsberg Pass, 4 055' [1 230 m], (–DA), shale flats in valley bottom, 9 Sept. 2006, *P. Goldblatt & L.J. Porter* 12805 (MO, NBG); Klein Roggeveld, near rest stop above Farm Fortuin, (–DA), 18 Sept. 2011, *P. Goldblatt & J.C. Manning* 13675 (MO, NBG); foot of Komsberg Pass, (–DA), 10 Sept. 2012, *J. Manning* 3376 (NBG); Farm De Plaat, N of homestead, 3 750' [1 130 m], (–DC), Karoo vegetation on sandy loam, 6 Sept. 1988, *A. Fellingham* 1393 (NBG, PRE).

WESTERN CAPE:—**3218** (Clanwilliam): Piquenierskloof [Pikenierskloof], (–DB), 6 Aug. 1897, *R. Schlechter* 10757 (BOL, PRE); Piketberg, Witwater, (–DC), 4 Oct. 1895, *H. Bolus* 8495

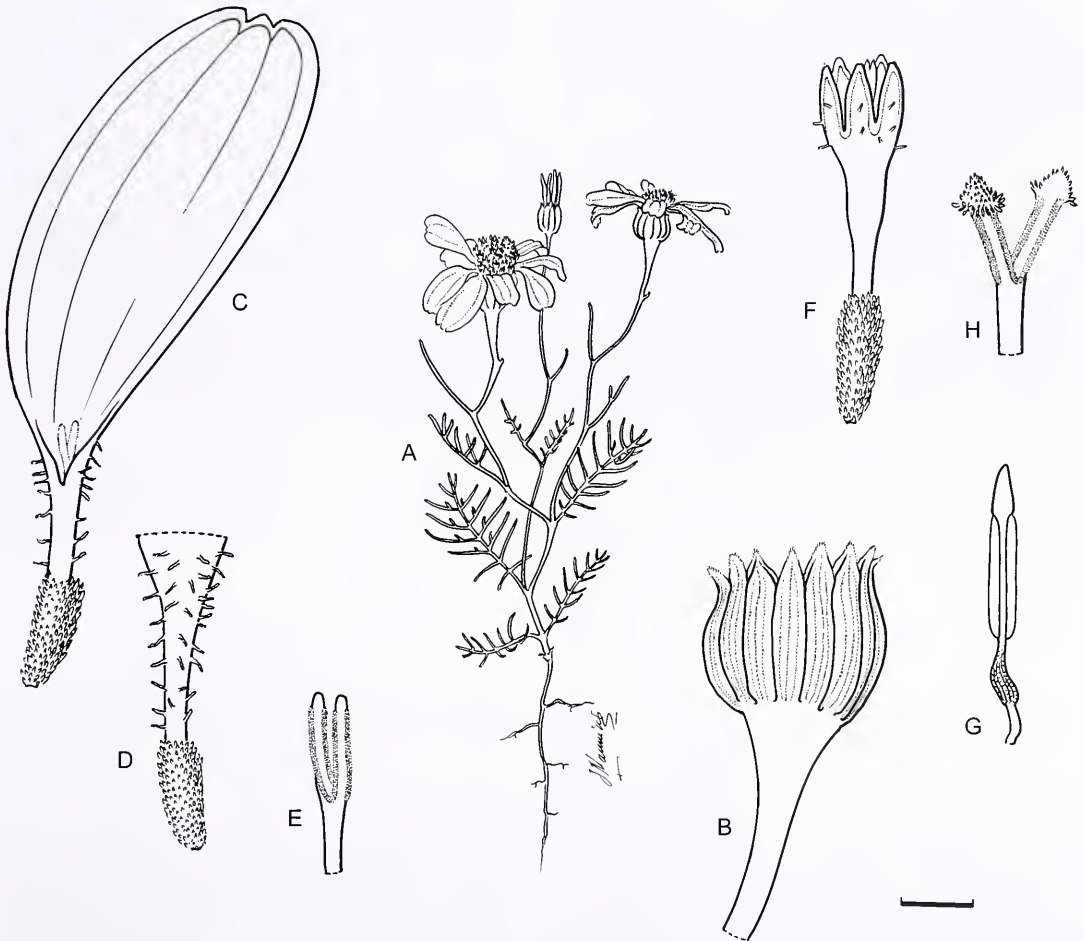


FIGURE 1.—*Steirodiscus capillaceus*, Manning 3376. A, plant; B, involucre; C, ray floret; D, ray floret detail of abaxial side of tube; E, ray floret stigma; F, disc floret; G, disc floret anther; H, disc floret stigma. Scale bar: A, 10 mm; B, 2 mm; C, D, F, 1 mm; E, G, H, 0.5 mm. Artist: J. Manning.



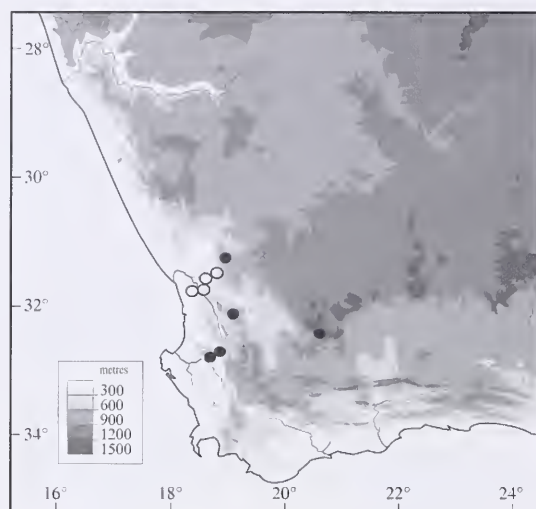


FIGURE 2.—Distribution of *Steirodiscus capillaceus*, ●; and *S. linearilobus*, ○.

(NBG, PRE), 3219 (Wuppertal): Koudeberg, (–AA), 28 Aug. 1896, *R. Schlechter* 8721 (BOL, PRE); Bidouw, (–AA), 7 Sept. 1953, *R.H. Compton* 24232 (NBG); Wuppertal, (–AC), 20 Aug. 1959, *W.F. Barker* 8992 (NBG); gate at entrance to Wuppertal property, (–AC), 8 Sept. 1974, *P. Goldblatt* 2530 (MO, NBG); Braakfontein [Citrusdal], (–?CA), 11 Sept. 1894, *R. Schlechter* 5282 (PRE), 3318 (Cape Town); near Hopefield, (–AB), Sept. 1905, *H. Bolus* 12706 (BOL).

2. *Steirodiscus linearilobus* DC., *Prodromus systematis naturalis regni vegetabilis* 6: 74 (1838 '1837'). Type: South Africa, Olifantsrivier, Knakarberg [Knakkiesberg], foot of hills, July 1839, *Drege s.n.* (G–DC, holo.—microfiche!; E, HAL, HBG, K, iso.—ALUKA images!).

*Steirodiscus schlechteri* Bolus: 217 (1899), syn. nov. *Psilothonna schlechteri* (Bolus) E.P. Phillips: 17 (1950). Type: South Africa, [Western Cape], Vanrhynsdorp Dist., Windhoek [Farm], 31 July 1896, *R. Schlechter* 8358 (BOL, holo.!; S, iso.).

Annual herb, 60–150 mm, stem strongly flexuous, corymbosely branched above. *Leaves* alternate, ascending, mostly 20–60 × 15–20(–35) mm, pinnatisect or bipinnatisect, with up to 10 lobes on each side, lobes alternate or subopposite and subsecund, filiform to linear, 3–15 × 0.5 mm, entire or with 1 or 2 lobules, uppermost leaves usually pinnatisect, sometimes simple and filiform. *Capitula* solitary, pedunculate; peduncles 20–50 mm long, with 2 or 3 minute, scale-like bracts. *Involucre* cylindrical to subglobose, 4–5 × 4–5 mm, bracts 13–16, free, convex abaxially and canaliculate adaxially, leathery and three-veined in basal two-thirds, with membranous margins, penicillate. *Ray florets* fewer than involucre bracts, 7–10, yellow; tube cylindrical, 2.5 mm long, with abaxial trichomes near top; blade 7–10 × 1.5–2.0 mm, spreading, recurved apically; ovary terete with slightly thickened distal collar, 1.5 mm long, glabrous, style branches exserted, 1 mm long. *Disc florets* bisexual, yellow, 5 mm long; tube funnel-shaped, ± 3 mm long; lobes ± 1 mm long, ovate, acute; ovary terete, 1.5 mm long, glabrous, style branches 1 mm long. *Cypselas* unknown. *Flowering time*: Aug. (Sept.). Figure 3.

*Distribution and ecology*: only rarely collected, *Steirodiscus linearilobus* is a local endemic of the lower reaches of the Olifants River and adjacent flats south and east of Vanrhynsdorp, recorded from the Knakkiesberg west of Klawer, northeastwards to the foot of the Koebe Mountains (Figure 2). The species occurs on sandy flats in open shrubland, including Klawer Sandy Shrubland (Mucina & Rutherford 2006).

*Diagnosis and relationships*: *Steirodiscus linearilobus* is distinguished from *S. capillaceus* by its glabrous ovaries and cypselas, and by its glabrous disc florets. The ray florets are slightly fewer than the involucre bracts, which number 13–16 vs. 8–12 in *S. linearilobus*, and the uppermost leaves are either simple or pinnatisect, but invariably simple in *S. capillaceus*.

*Steirodiscus linearilobus* was described from a collection made by Drège at the base of the Knakkiesberg, an inselberg west of Klawer (Candolle 1838) but the name was inexplicably overlooked by Phillips (1950) in his review of the genus (as *Psilothonna*). A later collection from just east of Klawer formed the basis for *Steirodiscus schlechteri* (Bolus 1899), separated from *S. linearilobus* essentially by its glabrous ovaries. The vestiture of the ovaries in *S. linearilobus* is not mentioned in the protologue and its identity has remained uncertain until now. It is only through the kindness of Mark Newman at the Royal Botanic Garden, Edinburgh, who dissected the Edinburgh isotype and confirmed that the ovaries of Drège's collection are glabrous (Newman pers. com.), that we are able to establish firmly that the two names are conspecific. Bolus (1899) distinguished *S. schlechteri* from *S. linearilobus* (and *S. capillaceus*) by its stouter habit, smaller leaves, larger heads, and glabrous achenes, but this is evidently just a general diagnosis of the species rather than an implication that the ovaries in *S. linearilobus* are pubescent. This implied pubescence of the ovaries in *S. linearilobus* led Hutchinson (1946) to misapply the name to his collection of *S. capillaceus* from the Klein Roggeveld.

*Conservation status*: *Steirodiscus linearilobus* is a local endemic known historically from just four localities in close proximity to one another. The only recent collection is from the verge of the N7 motorway south of Klawer.

#### *Additional specimens seen*

WESTERN CAPE.—3118 (Vanrhynsdorp): Urionskraal, (–DB), 4 Sept. 1955, *W.F. Barker* 8569 (NBG); sandy flats near foot of Tigerberg [Tierberg], 4 Sept. 1955, *G.J. Lewis* 4665 (SAM); Klawer, (–DC), Oct. 1917, *Roberts & Adendorff* 17685 (PRE); Van Rhynsdorp Road near Klawer, (–DC), Aug. 1932, *M. Lavis* 20259 (BOL); ± 5 km S of Klawer, cutting on N7, (–DC), 24 Aug. 2012, *J. Manning* 3367 (NBG).

*Uncertain locality*: Namaqualand, Aug. 1931, *J.W. Mathews s.n.* (BOL).

sect. *Psilothonna* (*E. Mey ex DC.*) *J.C. Manning & Goldblatt*, comb. nov. *Ganolepis* sect. *Psilothonna* *E. Mey ex DC.*: 40 (1838). Type species: *S. tagetes* (L.) Schltr.

Stems weakly or more strongly flexuous; involucre campanulate or obconic with bracts connate ± two-thirds in a smooth cup.



FIGURE 3.—*Steirodiscus linearilobus*, Manning 3367. A, plant; B, involucre; C, detached involucral bracts, abaxial view; D, fruiting involucre; E, ray floret; F, ray floret detail of abaxial side of tube; G, ray floret trichome (much enlarged); H, ray floret stigma; I, disc floret; J, disc floret anther; K, disc floret stigma. Scale bar: A, 10 mm; B, D, 2 mm; C, E, F, I, 1 mm; H, J, K, 0.5 mm. Artist: J. Manning.

3. *Steirodiscus tagetes* (L.) Schltr. in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie: 216 (1899), in obs. *Othonna tagetes* L.: 1234 (1758). *Gamolepis annua* Less.: 251 (1832), nom. illegit. superfl. *Gamolepis tagetes* (L.) DC.: 40 (1838 '1837'). *Psilothonna tagetes* (L.) E.P.Phillips: 17 (1950). Type: South Africa, without locality or collector. Herb. Linn. 1038.1 [LINN—ALUKA image!], lecto., designated by Nordenstam in Jarvis: 716 (2007).

Annual herb, (50–)100–200 mm, stem flexuous, corymbosely branched above. *Leaves* alternate, ascending, mostly  $30\text{--}60 \times 15\text{--}20$  mm, pinnatisect or some leaves rarely bipinnatisect, with up to 8 lobes on each side, lobes alternate or subopposite and subsecund, filiform to oblong,  $5\text{--}12 \times 0.5\text{--}1.0$  (–1.5) mm, entire or with 1 or 2 lobules, uppermost leaves sometimes simple and linear-filiform. *Capitula* solitary, pedunculate; peduncles 10–60 mm long, with 2 or 3 minute, scale-like bracts.



*Involucre* campanulate, 5–8 × 4–5(–6) mm, bracts (8–)10–13(–15), connate for two-thirds their length, free parts lanceolate, with narrow membranous margins, penicillate. *Ray florets* as many as bracts and opposite them, 8–15, yellow or rarely pale orange; tube narrowly cylindrical, ± 3.5 mm long, with abaxial trichomes in transverse band at top of tube, trichomes fleshy and coalescent or palmate and forming distinct fimbriate collar at junction between tube and blade; blade 8–10 × 3–4 mm, spreading, recurved apically; ovary terete, 2.5 mm long, glabrous, longitudinally colliculate, style branches partly or fully exerted, ± 1 mm long. *Disc florets* bisexual, yellow, 6–7 mm long; tube narrowly funnel-shaped, ± 4.5 mm long, sparsely pubescent in distal half; lobes ± 1 mm long, ovate, acute; ovary terete, 2 mm long, glabrous, longitudinally colliculate, style branches ± 1 mm long. *Cypselas* obovoid-prismatic, ± 2.5 mm long, glabrous, longitudinally colliculate, obscurely 5-angled and 10-ribbed. *Flowering time*: Sept.–Oct. Figure 4.

*Distribution and ecology*: *Steirodiscus tagetes* is relatively widely distributed along the West Coast of Western Cape, from St Helena Bay to False Bay (Figure 5). There are historical records from the Cape Peninsula but the species is probably now extinct there. It occurs on sand dunes near the coast, typically in lightly disturbed situations in strandveld vegetation, especially Cape Flats Dune Strandveld, where it may be locally abundant.

*Diagnosis and relationships*: the most common member of sect. *Psilothonna*, *Steirodiscus tagetes* is distinguished by the characteristic compound trichomes on the ray florets. These palmate structures (Figure 4E) form a fleshy, collar-like fringe around the top of the corolla tube at the base of the limb (Figure 4C, D), and are readily visible with a hand lens. The capitula are typically larger than in *S. gamolepis* and *S. speciosus*, with a campanulate involucre 4–5 mm diam. It is superficially very similar to *S. speciosus*, but in this species the trichomes on the ray florets are not coalescent into compound structures and the involucre is generally smaller, 2–3 mm diam. The flowers in both species are typically bright yellow but may also be tinged orange. The species is variable in flower size with the largest and most attractive forms occurring west of Atlantis.

*Conservation status*: Once relatively widely recorded along the West Coast, *Steirodiscus tagetes* is now extinct from the Cape Peninsula and probably also around Langebaan as a result of the extensive urbanisation there. The only recent collections are those from Macassar and along the West Coast west of Atlantis.

#### *Additional specimens seen*

WESTERN CAPE.—3218 (Clanwilliam): ± 5 km S of St Helena, Franslei, 120 m, (–CC), 3 Sept. 2008, *N. Helme* 5643 (NBG); Berg River, (–CD), 21 Sept. 1940, *R.H. Compton* 9472 (NBG); Berg River Station, (–CD), in sand, 1 Oct. 1943, *R.H. Compton* 15105 (NBG). 3318 (Cape Town): Saldanha Bay, hillside, (–AA), 27 Sept. 1930, *E.E. Galpin* 11500 (PRE); hills NE of Langebaan, (–AA), Oct. 1933, *N.S. Pillans* 7005 (BOL); Geelbek road, (–AA), 28 Sept. 1953, *W.F. Barker* 8159 (NBG); near Langebaan, (–AA), 2 Oct. 1970, *M.R. Levyns* 11725 (BOL); near Hopefield, (–AB), 13 Sept. 1894, *R. Schlechter* 5322 (SAM); sand dunes on W coast opposite turnoff to Atlantis, (–CA), 11 Sept. 2004, *P. Goldblatt & L.J. Porter* 12395 (MO, NBG); R307 opposite Atlantis, (–CB), 29 Sept. 2012, *J. Manning* 3377 (NBG); W coast N of Atlantis turnoff, (–CB), 26 Sept. 1998, *P. Goldblatt & J. Manning* 11028 (MO, NBG); Melkbosch Strand, (–CB), 16 Oct. 1947,

*Schrieber s.n.* NBG24181 (NBG); sandy places, Paarden Eiland, Nov., without year, *Zeyher s.n.* (SAM); Cape Flats, Stikland, 62 m, (–DC), 30 Aug. 1979, *C. Boucher* 4501 (NBG); Cape Flats, (–DC), 16 Sept. 1944, *R.H. Compton* 15975 (NBG); between Brackenfell and Kraaifontein along road to Paarl, (–DC), 17 Sept. 1975, *E. Esterhuysen* 33975 (BOL); Cape Flats Nature Reserve, (–DC), 27 Oct. 1978, *A.B. Low* 738 (NBG). 3418 (Simonstown): Hout Bay, (–AB), 4 Sept. 1941, *R.H. Compton* 112289 (NBG); 3 Sept. 1950, *A.J. Middelmost* 1576 (NBG); Klipfontein Road, (–BA), sand dunes, 30 Aug. 1931, *M.R. Levyns* 3172 (BOL); coastal dunes between Eerste River and Swartklip, (–BA), 1 Oct. 1939, *N.S. Pillans* 9207 (BOL); Durban Road Station, (–CD), Sept. 1877, *H. Bolus* 3778 (BOL, SAM); near Retreat Station, (–AB), Sept. 1892, *H. Bolus* 7242 (BOL, PRE); Strandfontein, (–BA), 18 Sept. 1942, *R.H. Compton* 13697 (NBG); Somerset Strand, (–BB), 2 Oct. 1921, *G.C. Nel* 1282 (PRE); Macassar, Somehem, 20 m, (–BB), 28 Sept. 1995, *A.B. Louw* 2473 (NBG).

*Without precise locality*: ‘prope Piketberg’, Oct. 1892, *H. Bolus* 13575 (PRE); ‘prope Darling’, Sept. 1905, *H. Bolus* 12734 (PRE).

*Uncertain collections*: Groenekooft [Mamre], without date, *Zeyher s.n.* pp. (SAM); ‘Prom. bon. Spei, Driefontein’, Nov. without year, *Zeyher* 828 pp. (SAM) [These two collections by Zeyher include plants of both *S. tagetes* and *S. speciosus*, but as these are hopelessly muddled between the various duplicates it is unclear whether they were growing together or mixed up later].

4. *Steirodiscus speciosus* (Pillans) B.Nord. in Opera Botanica 20: 31 (1968), in obs. *Gamolepis speciosa* Pillans: 50 (1931). *Psilothonna speciosa* (Pillans) E.P. Phillips: 17 (1950). Type: South Africa, [Western Cape], between Darling and the coast, exhibited at Darling Show, Sept. 1929, collector unknown *Pillans sub BOL18965* (BOL, holo.!: K, iso.—ALUKA image!).

Annual herb, 80–300 mm, stem flexuous, corymbosely branched above. *Leaves* alternate, ascending, mostly 30–40 × 15–20 mm, pinnatisect or some leaves rarely obscurely bipinnatisect, with up to 7 lobes on each side, lobes alternate or subopposite and subsecond, filiform, 3–12 × 0.5 mm, entire or with 1 or 2 lobules, uppermost leaf sometimes simple and filiform. *Capitula* solitary, pedunculate; peduncles 20–40 mm long, with 1–3 minute, scale-like bracts. *Involucre* campanulate when fresh but drying urceolate with marked constriction above ovaries, 5–6 × 2–4 mm, bracts 11–15(–18), connate for two thirds their length, free parts lanceolate, with narrow membranous margins, penicillate. *Ray florets* ± as many as bracts and opposite them, 11–18, yellow or rarely pale orange; tube narrowly cylindrical, 2.0–3.5 mm long, with scattered abaxial trichomes at top of tube; blade 7–10 × 3–4 mm, spreading, recurved apically; ovary terete, 2.5 mm long, glabrous, longitudinally colliculate, style branches partly or fully exerted, ± 1 mm long. *Disc florets* bisexual, yellow, 4–5 mm long; tube narrowly funnel-shaped, 3–4 mm long, sparsely pubescent in distal half; lobes ± 1 mm long, ovate, acute; ovary terete, 2.5 mm long, glabrous, longitudinally colliculate, style branches ± 1 mm long. *Cypselas* obovoid-prismatic, ± 2.5 mm long, glabrous, longitudinally colliculate. *Flowering time*: Sept.–Oct. Figure 6.

*Distribution and ecology*: a highly local endemic of the West Coast between Darling and Atlantis (Figure 5), *Steirodiscus speciosus* is very poorly known. Described from plants collected between Darling and the coast





FIGURE 4.—*Steirodicus tagetes*, Manning 3377. A, plant; B, involucre; C, ray floret; D, ray floret detail of abaxial side of tube; E, ray floret trichome (much enlarged); F, ray floret stigma; G, disc floret; H, disc floret anther; I, disc floret stigma; J, ray cypsel; K, disc cypsel. Scale bar: A, 10 mm; B, 2mm; C, D, G, J, K, 1 mm; F, H, I, 0.5 mm. Artist: J. Manning.

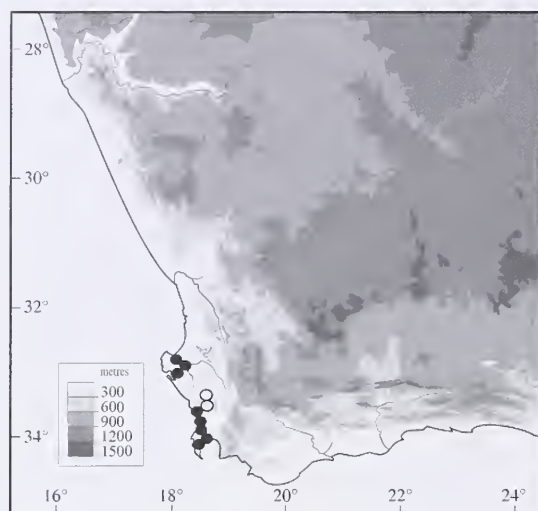


FIGURE 5.—Distribution of *Steirodiscus tagetes*, ●; and *S. speciosus*, ○.

and exhibited at the Darling Show in September 1929, the only recent collections of the species are from near Atlantis, where we have found it in deep sandy soils in sand plain fynbos, specifically Atlantis Sand Fynbos (Mucina & Rutherford 2006). The records for *S. speciosus* all fall within the distribution of this vegetation type and the species thus appears to be restricted to it. Germination in *S. speciosus* is evidently stimulated by light disturbance as we first encountered the species after a fire the previous summer and later along the roadside but have never seen it in mature vegetation.

**Diagnosis and relationships:** *Steirodiscus speciosus* is very similar to *S. tagetes* and was diagnosed against it by Pillans (1931) (as *G. annua*), and as having larger ( $\pm 18 \times 3.5\text{--}4.0$  mm), more numerous (14–23) orange rays lacking a distinct annulus of papillae around the mouth of the tube and with more strongly exerted styles. Most of these characters do not hold, even in the type of *S. speciosus*, which has up to 15 rays that are no larger than are found in most populations of *S. tagetes* and also does not differ in the styler characters. Although the specific status of the taxon was questioned in 1933 by R.A. Dyer (letter on K isotype), Phillips (1950) accepted the species in his synopsis of the genus (as *Psilothonna*), but keyed it against *S. tagetes* solely on the absence (vs. presence) of ‘glands’ at the base of the rays. Both taxa, like all species in the genus, have multicellular trichomes (‘glands’) at the top of the ray corolla tube on the abaxial (outer) side and the critical difference between them is in the nature of the trichomes themselves. In *S. tagetes* the trichomes coalesce into compound, palmate structures (Figure 4E) that form a fimbriate collar around the corolla tube (Figure 4C, D) whereas in *S. speciosus* the individual trichomes remain discrete (Figure 6C, D). *S. speciosus* is also distinguished by its smaller involucre, 2–4 mm diam., which constricts markedly above the ovaries as it dries, giving it a characteristic urceolate shape in herbarium specimens (Figure 6B). This is not evident in fresh material, at which time the distinction between the two species is

more cryptic, requiring careful examination of the ray floret vestiture with a hand lens. Ecologically *S. speciosus* appears to favour sand plain fynbos (this remains to be confirmed for additional populations) whereas *S. tagetes* is definitely restricted to strandveld vegetation along the coast.

**Conservation status:** *Steirodiscus speciosus* is a highly local endemic with just a single recent collection near Atlantis, where it is under immediate threat from urbanisation.

#### *Additional specimens seen*

**WESTERN CAPE.**—**3318** (Cape Town): Darling, (–AC), 16 Oct. 1942, *Mrs W.M. Duckitt* NBG24186 (NBG); near Darling, (–AC), Sept. 1946, *T.P. Stokoe* SAM59958 (SAM); 11 Sept. 1950, *M. Johns* NBG 24185 (NBG); Mamre Road, (–BC), sand, 2 Oct. 1931, *M.R. Levyns* 3269 (BOL); sandy flats 2 miles [3 km] S of Mamre, (–CB), 1 Sept. 1940, *N.S. Pillans* 9255 (BOL). **3320** (Cape Town): between Melkbos and Mamre, (–CB), 1932, *L. Bolus* s.n. PRE43910 (PRE); 16 km along Mamre road from turn-off on Melkbosstrand road, (–CB), 23 Sept. 1974, *Nordenstam & Lundgren* 1986 (S); sandy flats near Atlantis, S of Mamre, (–CB), bright orange flowers, 27 Sept. 1995, *P. Goldblatt & J. Manning* 10334 (MO, NBG); 500 m S of Mamre–Atlantis T-junction, (–CB), 10 Oct. 2012, *J. Manning & Goldblatt* 3383 (NBG).

**Uncertain collections:** Groenekoof [Mamre], without date, *Zeyher* s.n. pp. (SAM); Rietvley [Rietvlei], without date, *Zeyher* 1679 (BOL, NBG); ‘Prom. bon. Spei, Driefontein’, Nov. without year, *Zeyher* 828 pp. (BOL, NBG, SAM). [These three collections by Zeyher include plants of both *S. tagetes* and *S. speciosus* but as these are hopelessly muddled between the various duplicates, it is unclear whether they were growing together or mixed up later].

**5. *Steirodiscus gamolepis* Bolus** in Schltr. in Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 27: 216 (1899). *Psilothonna gamolepis* (Bolus) E.P. Phillips: 17 (1950). Type: South Africa, [Western Cape], Ceres Road, 11 Sept. 1896, *R. Schlechter* 8974 (BOL, lecto!, designated here; BR, E, HBG, K, M, P, PRE, S, isolecto.—ALUKA images!). [Syntype: South Africa, [Western Cape], Tulbagh Kloof, 30 Sept. 1892, *H. Bolus* 8605 (BOL!, NBG!, NH, PRE, syn.). [The Schlechter collection is selected as lectotype as being better represented in herbaria internationally.]

Annual herb, 60–130 mm, stem flexuous, simple or sparsely corymbosely branched above. *Leaves* alternate, ascending, mostly 10–20 × 5–10 mm, trisect or pinnatisect, with 1–3 lobes on each side, lobes alternate or opposite and subsecund, filiform, 1–5 × 0.5 mm, uppermost leaves simple and filiform. *Capitula* solitary, conspicuously pedunculate; peduncles 30–60 mm long, with 1 or 2 minute, scale-like bracts. *Involucre* narrowly campanulate or obconic, 3.5–4.5 × 1.5–3.0 mm, bracts 10–14, connate for two thirds their length, free parts lanceolate, with narrow membranous margins, penicillate. *Ray florets*  $\pm$  half as many as bracts, 4–8, yellow; tube narrowly cylindrical, 2 mm long, with scattered abaxial trichomes at top of tube extending onto base of blade; blade 6–8 × 2–3 mm, spreading, recurved apically; ovary terete, 2 mm long, antrorsely pubescent in basal two thirds, style branches exerted,  $\pm$  0.75 mm long. *Disc florets* bisexual, yellow, 3 mm long; tube funnel-shaped, 2 mm long, glabrous; lobes  $\pm$  1 mm long, ovate,

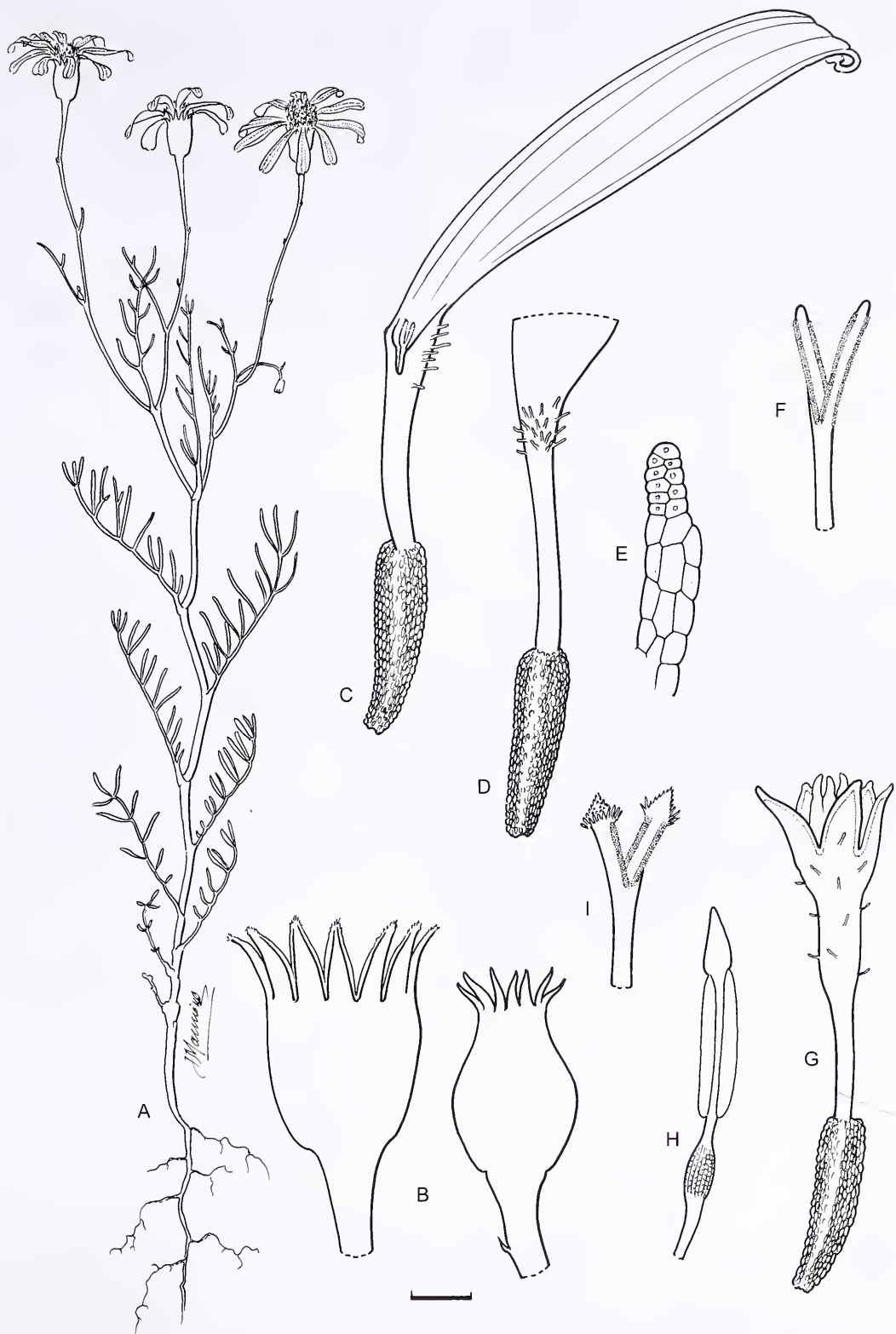


FIGURE 6.—*Steirodicus spectosus*, Manning & Goldblatt 3383. A, plant; B, involucre, fresh (left) and dried (right); C, ray floret; D, ray floret detail of abaxial side of tube; E, ray floret trichome (much enlarged); F, ray floret stigma; G, disc floret; H, disc floret anther; I, disc floret stigma. Scale bar: A, 10 mm; B, 2mm; C, D, G, 1 mm; F, H, I, 0.5 mm. Artist: J. Manning.



acute; ovary terete, 2 mm long, antrorsely pubescent in basal two thirds, style branches 0.5 mm long. *Cypselas* flask-shaped (ray) or terete (disc),  $\pm 2$  mm long, antrorsely pubescent in basal two thirds. *Flowering time*: Aug.–Sept. Figure 7.

*Distribution and ecology*: *Steirodiscus gamolepis* is restricted to the flats at the foot of the Elandsbloof Mountains near Tulbagh (Figure 8) and remained very poorly known until recent collections established its occurrence on Elandsberg Nature Reserve, where it is now best known. The type from Ceres Road appears to come from the Tulbagh Valley itself, but other records are from the western side of the mountains between Gouda and Hermon. At Elandsberg Nature Reserve, *S.*

*gamolepis* is locally abundant on seasonally wet gravelly flats in alluvium fynbos shrubland, and available data suggests that the species is endemic to Swartland Alluvium fynbos and possibly also Breede Alluvium Fynbos (Mucina & Rutherford 2006).

*Diagnosis and relationships*: The smallest species in the genus, *Steirodiscus gamolepis* is distinctive in its short, few-lobed leaves and diminutive, markedly pedunculate capitula with the peduncle grading into the narrowly campanulate or obconic involucre. The rays are relatively few, up to half as many as the involucre lobes, and the ovaries and cypselas are pubescent in the basal two thirds but glabrous above. The corollas of the disc florets are glabrous and unique in the genus in the

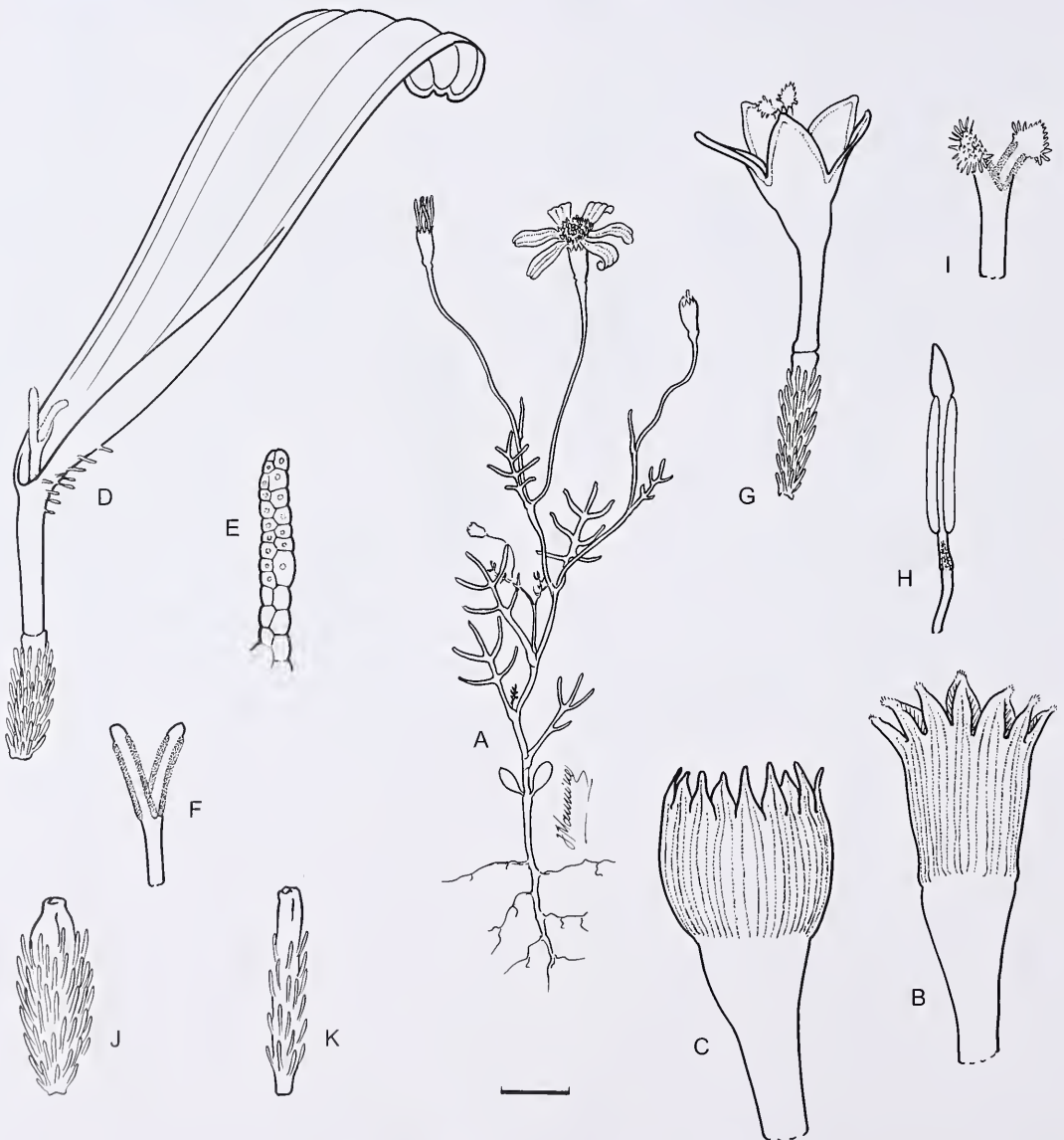


FIGURE 7.—*Steirodiscus gamolepis*, Manning 3366A. A, plant; B, involucre; C, fruiting involucre; D, ray floret; E, ray floret trichome (much enlarged); F, ray floret stigma; G, disc floret; H, disc floret anther; I, disc floret stigma; J, ray cypsel; K, disc cypsel. Scale bar: A, 10 mm; B, C, 2mm; D, G, J, K, 1 mm; F, H, I, 0.5 mm. Artist: J. Manning.

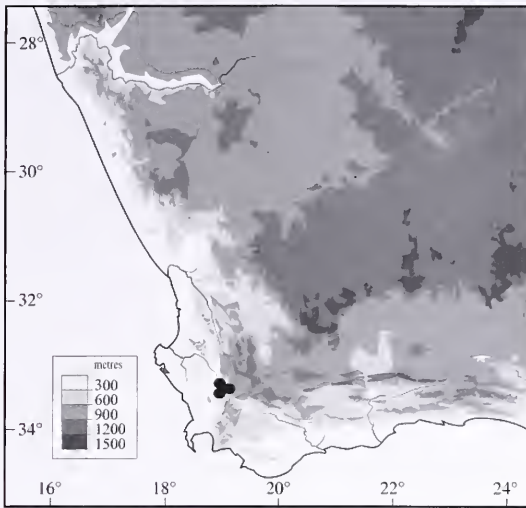


FIGURE 8.—Distribution of *Steirodiscus gamolepis*, ●.

short upper expanded portion of the perianth tube, much shorter than both the cylindrical lower portion and the lobes. Other members of sect. *Psilothonna* are larger in all respects, with less conspicuous peduncles that are sharply differentiated from the involucre,  $\pm$  as many rays as involucre lobes, disc florets that are sparsely puberulous on the corolla, with the upper expanded portion  $\pm$  as long as the lobes and the lower portion, and glabrous ovaries and cypselas. The peduncles in *S. gamolepis* are unusually tough and wiry. The seasonally inundated habitat is unique in the genus, other species preferring drier, mostly sandy flats.

**Conservation status:** *Steirodiscus gamolepis* is a highly local endemic known to persist only at Elandsberg Nature reserve, where it is still relatively plentiful.

#### Additional specimens seen

WESTERN CAPE.—3319 (Worcester): flats near Piquetberg Station, (–AA), Oct. 1892, *F. Guthrie 2624b* (NBG); Elandsberg Farm and Nature Reserve, (–AC), 24 Aug. 2009, *L. Husted 780* (NBG); Bo-Hermon, Elandsberg Nature Reserve, (–AC), 15 Oct. 2011 [fruiting], *Manning 3359* (NBG); 15 Oct. 2011, *J. Manning 3359* (NBG); 10 Aug. 2012, *J. Manning 3366A* (NBG).

#### ACKNOWLEDGEMENTS

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## OBITUARY

SARIE MAGDALENA PEROLD (1928–2011)

Sarie Perold (née Lombard) (Figure 1) was born in Johannesburg, South Africa on 19 May 1928 and died in a frail care centre near Pretoria on Friday 11 November 2011, aged 83.

Dr or Mevrouw [Mrs.] Perold, as I used to call her, for she hated being called by her first name by strangers and anyone she perceived as her junior, matriculated from the Kensington Hoërskool in 1945 with four distinctions. She studied at the University of the Witwatersrand (Wits) and received a B.Sc. degree in 1949, majoring in Anatomy and Histology. She well remembered the large first year classes at Wits as a result of the return of ex-servicemen from World War II. From 1950 to mid 1967, she worked as a laboratory technician in Histology and Chemical Pathology at the South African Institute for Medical Research, then for Irving & Robertson, a firm of private pathologists, and finally as a research assistant in the Department of Chemical Pathology at the Wits Medical School.

In 1953 she married the writer and film director Jan Perold, known for Afrikaans feature films such as *Die ruiter in die nag* (1963). Their only child, Jan, was born in 1967 and a year later they moved from Linden in Johannesburg to Val-de-Grace in Pretoria. Re-entering the work force in 1976, Dr Perold held several temporary teaching posts at private and public schools in Pretoria. During this time she also completed second year



FIGURE 1.—Sarie Magdalena Perold (1928–2011). Photograph: Elizma Fouché.



FIGURE 2.—Sarie Perold at work in the PRE bryophyte herbarium shortly after she started there in 1980. Photograph: Adela Romanowski.

courses in Zoology and Botany at the University of Pretoria. Her lecturers included the legendary Mr Oosthuizen of Zoology and Prof. Braam van Wyk, who later served as study leader for both her master's and doctoral degrees (Perold 1990, 1991). Little did she know that she herself would one day present a course on Bryology to 2<sup>nd</sup> year Botany students at the University of Pretoria; from 1992 to 1997.

In November 1979, Dr Perold joined the Botanical Research Institute (later the National Botanical Institute and now the South African National Biodiversity Institute) as a PRECIS database encoder. This job was very convenient, as she lived close to the botanical gardens and could drive her son to his many extra-mural activities in the afternoons. She also loved driving through the gardens on her way to work in the mornings. However, the encoding did not agree with her and she requested a transfer to the downtown head office of the Department



FIGURE 3.—From left, Jacques van Rooy, Robert (Bob) Magill and Sarie Perold in the PRE bryophyte herbarium, Oct. 1994. Photograph: Adela Romanowski.

Table 1. Liverwort taxa published by Sarie M. Perold (as listed in Tropicos, botanical information system at the Missouri Botanical Garden: [www.tropicos.org](http://www.tropicos.org))

Family	Name	Author	Reference	Date
Aytoniaceae	<i>Cryptomitrium oreades</i>	Perold	<i>Bothalia</i> 24: 149. f. 1–2	1994
Fossombroniaceae	<i>Fossombronia angulifolia</i>	Perold	<i>Bothalia</i> 28: 159. f. 1–3	1998
Fossombroniaceae	<i>Fossombronia capensis</i> var. <i>spiralis</i>	Perold	<i>Bothalia</i> 29: 1. f. 1–3	1999
Fossombroniaceae	<i>Fossombronia cederbergensis</i>	Perold	<i>Bothalia</i> 28: 1. f. 1–3	1998
Fossombroniaceae	<i>Fossombronia elsiae</i>	Perold	<i>Bothalia</i> 29: 25. f. 1–3	1999
Fossombroniaceae	<i>Fossombronia gemmifera</i>	Perold	<i>Bothalia</i> 27: 19. f. 1–3	1997
Fossombroniaceae	<i>Fossombronia glenii</i>	Perold	<i>Bothalia</i> 27: 20. f. 5–7	1997
Fossombroniaceae	<i>Fossombronia hyalorhiza</i>	Perold	<i>Bothalia</i> 29: 83. f. 1–3	1999
Fossombroniaceae	<i>Fossombronia marindae</i>	Perold	<i>Bothalia</i> 29: 86. f. 5–7	1999
Fossombroniaceae	<i>Fossombronia monticola</i>	Perold	<i>Bothalia</i> 29: 87. f. 8–10	1999
Fossombroniaceae	<i>Fossombronia nyikaensis</i>	Perold	<i>Bothalia</i> 31: 48	2001
Fossombroniaceae	<i>Fossombronia renateae</i>	Perold	<i>Bothalia</i> 29: 77. f. 1–3	1999
Fossombroniaceae	<i>Fossombronia rwandaensis</i>	Perold	<i>Bothalia</i> 28: 45. f. 1–7	1998
Fossombroniaceae	<i>Fossombronia spinosa</i>	Perold	<i>Bothalia</i> 29: 29. f. 5–8	1999
Fossombroniaceae	<i>Fossombronia straussiana</i>	Perold	<i>Bothalia</i> 27: 24. f. 8–10	1997
Fossombroniaceae	<i>Fossombronia swaziensis</i>	Perold	<i>Bothalia</i> 28: 162. f. 5–7	1998
Fossombroniaceae	<i>Fossombronia zuurbergensis</i>	Perold	<i>Bothalia</i> 31: 25	2001
Ricciaceae	<i>Riccia</i> subgen. <i>Chartaceae</i>	Perold	<i>Bothalia</i> 16: 29	1986
Ricciaceae	<i>Riccia</i> sect. <i>Micantes</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 187	1986
Ricciaceae	<i>Riccia</i> sect. <i>Pannosae</i>	Perold	<i>Bothalia</i> 20: 28	1990
Ricciaceae	<i>Riccia alatospora</i>	O.H. Volk & Perold	<i>Bothalia</i> 15: 534. f. 4–6	1985
Ricciaceae	<i>Riccia alatospora</i> var. <i>hantamensis</i>	Perold	<i>Hist. Phys. Cuba, Bot., Pl. Cell.</i>	?
Ricciaceae	<i>Riccia alborosa</i>	Perold	<i>Bothalia</i> 19: 12. f. 5–6	1989
Ricciaceae	<i>Riccia albornata</i>	O.H. Volk & Perold	<i>Bothalia</i> 18: 160. f. 6–8	1988
Ricciaceae	<i>Riccia ampullacea</i>	Perold	<i>Bothalia</i> 20: 168. f. 1–3	1990
Ricciaceae	<i>Riccia argenteolimbata</i>	O.H. Volk & Perold	<i>Bothalia</i> 18: 155. f. 1–3	1988
Ricciaceae	<i>Riccia atlantica</i>	Sérgio & Perold	<i>J. Bryol.</i> 17: 127. f. 1–3	1992
Ricciaceae	<i>Riccia bicolorata</i>	Perold	<i>Bothalia</i> 20: 187. f. 5–7	1990
Ricciaceae	<i>Riccia biokoensis</i>	Perold	<i>Nova Hedvigia</i> 64: 244. f. 1–13	1997
Ricciaceae	<i>Riccia duthieae</i>	O.H. Volk & Perold	<i>Bothalia</i> 15: 531. f. 1–3	1985
Ricciaceae	<i>Riccia elongata</i>	Perold	<i>Bothalia</i> 20: 167. f. 1–3	1990
Ricciaceae	<i>Riccia erubescens</i>	Perold	<i>J. Bryol.</i> 16: 371. f. 4–6	1991
Ricciaceae	<i>Riccia furfuracea</i>	Perold	<i>Bothalia</i> 20: 176. f. 1–3	1990
Ricciaceae	<i>Riccia hantamensis</i>	Perold	<i>Bothalia</i> 19: 157. f. 2–4: A–F: a	1989
Ricciaceae	<i>Riccia hirsuta</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 187. f. 1–3	1986
Ricciaceae	<i>Riccia mamnifera</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 176. f. 8–10	1986
Ricciaceae	<i>Riccia mamrensis</i>	Perold	<i>Cryptog. Bryol.</i> 26: 68	2005
Ricciaceae	<i>Riccia microciliata</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 173. f. 5–7	1986
Ricciaceae	<i>Riccia montana</i>	Perold	<i>Bothalia</i> 19: 9. f. 1–3	1989
Ricciaceae	<i>Riccia namaquensis</i>	Perold	<i>Bothalia</i> 20: 180. f. 8–10	1990
Ricciaceae	<i>Riccia parvoareolata</i>	O.H. Volk & Perold	<i>Bothalia</i> 15: 117. f. 1–3	1984
Ricciaceae	<i>Riccia pulveracea</i>	Perold	<i>Bothalia</i> 20: 185. f. 1–3	1990
Ricciaceae	<i>Riccia radiata</i>	Perold	<i>Bothalia</i> 34: 23	2004
Ricciaceae	<i>Riccia rosea</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 181. f. 1–4	1986
Ricciaceae	<i>Riccia sarcosa</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 23. f. 1–4	1986
Ricciaceae	<i>Riccia schelpei</i>	O.H. Volk & Perold	<i>Bothalia</i> 16: 29. f. 1–3	1986
Ricciaceae	<i>Riccia sibayenii</i>	Perold	<i>Bothalia</i> 31: 151	2001
Ricciaceae	<i>Riccia simii</i>	Perold	<i>Bothalia</i> 20: 36. f. 5–7	1990
Ricciaceae	<i>Riccia somaliensis</i>	Perold	<i>J. Bryol.</i> 16: 367. f. 1–3	1991
Ricciaceae	<i>Riccia stricta</i>	(Gottsche, Lindenb. & Nees) Perold	<i>Bothalia</i> 20: 197	1990
Ricciaceae	<i>Riccia tomentosa</i>	O.H. Volk & Perold	<i>Bothalia</i> 20: 25. f. 1–2, 3–6	1990
Ricciaceae	<i>Riccia trachyglossum</i>	Perold	<i>Bothalia</i> 20: 172. f. 8–10	1990
Ricciaceae	<i>Riccia vitrea</i>	Perold	<i>Bothalia</i> 20: 178. f. 5–7	1990
Ricciaceae	<i>Riccia vitrenosa</i>	Perold	<i>Index Bryol.</i> (ed. 2)	?

of Agriculture. Fortunately, the personnel officer, Mrs. Gwen Hussem, realised that it would be a loss for the institute and organised a post for her in the herbarium, as part-time technical assistant to Dr Robert (Bob) Magill (Figure 3). He was on contract from the Missouri Botanical Garden to revise the mosses for the *Flora of south-*





FIGURE 4.—Collecting bryophytes in Lesotho as part of the first overseas British Bryological Society taxonomic workshop: National University of Lesotho (NUL), Roma, Apr. 1997. From left, Mr T. Mafa, Prof. Jeff Duckett, Dr A. Motecette, Dr Sarie Perold and Mr Howard Matcham. Photograph: Marinda Koekemoer.

ern Africa (FSA) project. Her duties included microscope slide preparation, physical and scientific curation, identifications, and later taxonomic research (Figure 2). She was also in charge of the institute's Scanning Electron Microscope unit for many years.

How she landed this job in the first place came to light years later in a note addressed to Dr Donald Killick, Deputy Director of the institute, dated 28 April 1989. She wrote 'I would like to take this opportunity of sincerely thanking you for interviewing and appointing me ten years ago, when Mrs. Bruyns contacted you on my behalf. I have been very happy in my work at BRI.' On the 2<sup>nd</sup> of May Dr Killick replied 'I can't remember interviewing you, but if I did, it was one of the best appointments made.'

Dr Perold had many interesting stories to tell about her employers but always concluded that SANBI was the best place she ever worked for. Her great sense of humour kept us going through difficult times. In the words of a retired ex-curator of the National Herbarium: 'herbarium is dogsbody'. Her main regret was that she was always in only a 'temporary' post.

So she embarked upon a career in bryology at the relatively late age of 51, but nevertheless became one of the leading experts on the taxonomy and nomenclature of African thallose liverworts, in particular the genus *Riccia* (Van Rooy 2012). Dr Perold published more than 100 botanical papers, at nearly five papers per year, the vast majority of which appeared in SANBI's house journal *Bothalia* (see list below). Her longest series in *Bothalia* is *Studies in the genus Riccia (Marchantiales) from southern Africa* with 27 papers. However, she also published in several overseas journals, often by invitation (Van Rooy 2012). Her work on the thallose liverworts (Order Marchantiales) culminated in the first fascicle of the liverwort volume in the FSA series (Perold 1999). Dr Perold is the author or co-author of 53 new liverwort

names (36 in the family Ricciaceae) and one new combination (Table 1). She collected more than 5 000 numbers in South Africa, Lesotho (Van Rooy 2012) (Figure 4), Swaziland, Malawi, Réunion and Zimbabwe.

In 1993, when she reached the age of 65, Dr Perold had to retire from SANBI, but was determined to continue with her research. She was annually re-appointed on a temporary, part-time basis for another decade. Thereafter she maintained an active presence in her office and finally retired from scientific work in June 2009.

Dr Perold was a member of the International Association of Bryologists (IAB) for many years. She served on the International Association for Plant Taxonomy (IAPT) permanent Nomenclature Committee for Bryophytes from 2000 to 2005. In 1992, she was awarded the R.A. Dyer Prize for her contribution to taxonomic research at SANBI. The following year she received the Junior Captain Scott Medal, awarded by the South African Academy for Science and Arts for the best M.Sc. dissertation at a South African University. In 2011, the year of her death, she received the South African Association of Botany Silver Medal for her significant contributions to the advancement of botany in South Africa. In his endorsement of her nomination, Prof. Braam van Wyk concluded that '*Dr Perold is undoubtedly the most eminent hepaticologist southern Africa has hitherto produced. Her contributions to the taxonomy of the liverworts of Africa in general and southern Africa in particular have been immense and in many instances pioneering. All her scientific contributions are of the highest standard and of lasting significance.*'

Life wasn't all about liverworts to Dr Perold. She delighted in the presence of bush babies, small nocturnal primates (*Galego moholi*), that were living in the trees around her house. She regularly put out fruit for them, especially bananas. She also kept a pet squirrel monkey (*Saimiri* sp.) called Kesie, that she showered with love.



Kesie was let loose in the trees around her house in the afternoons, to the dismay of her neighbours. After the monkey had died, she adopted a stray kitten. She particularly loved a little Scrophulariaceae plant, *Cymbalaria muralis* subsp. *muralis* (ivy-leaved toadflax). She gave a plant to a friend to look after, to ensure she did not lose it.

Dr Perold's funeral service was held in the Nederduitse Gereformeerde Kerk, Skuilkrans, just down the road from the institute, on 18 November 2011. It was attended by many relatives, friends and former colleagues, including Mrs. Girlie Filter and me, both technical assistants in the bryophyte herbarium at the time of her appointment. She is survived by her son Jan, a research psychologist.

In his letter of condolence, Prof. Rod Seppelt of Tasmania, a long-time correspondent, wrote '*She will be a great loss and her contributions to our knowledge of the South African hepatic flora have been exemplary.*' The eminent bryologists and experts on the bryoflora of Africa, Prof. Ryzard Ochrya and his wife Prof. Halina Bednarek-Ochrya from Krakow, Poland, remarked that '*Her death is a great loss, not only for South African but also international bryology and her meticulous work on thallose hepatics will continue to serve as a model of unprecedented scrutiny and accuracy.*'

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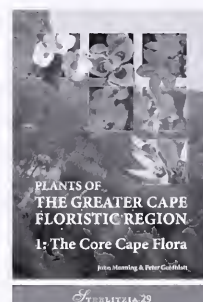
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